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Molluscan types of the *Albatross* Expeditions to the Eastern Pacific described by W. H. Dall (1908)

ALAN R. KABAT

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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MOLLUSCAN TYPES OF THE *ALBATROSS* EXPEDITIONS TO THE EASTERN PACIFIC DESCRIBED BY W. H. DALL (1908)

ALAN R. KABAT[1]

ABSTRACT. This paper documents the type material of 215 species of mollusks described by W. H. Dall in his 1908 monograph on the shelled mollusks and brachiopods collected by Alexander Agassiz during the three cruises of the *Albatross* in the tropical Pacific. The division of type specimens between Harvard University (Museum of Comparative Zoology) and the Smithsonian Institution (U.S. National Museum), as well as other curatorial problems, has resulted in some errors and omissions in the subsequent literature. These are here rectified.

INTRODUCTION

Alexander Agassiz [1835–1910], the founder of oceanographic research in the United States and second director of the Museum of Comparative Zoology (MCZ) at Harvard College, had three major series of expeditions to his name: first, the three cruises of the *Blake* (1877–80) in the western Atlantic, primarily in the Caribbean Sea and Gulf of Mexico; second, several cruises (on various small steamers) in the western Pacific and the Indian Ocean at the turn of the century; and third, the three cruises of the *Albatross* in the tropical eastern Pacific (1891, 1899–1900, 1904–05). Specifically, the first *Albatross* cruise went from Panama to the Galápagos Islands, to Acapulco, and then to the Gulf of California; the second went from San Francisco to the Marquesas and thence westward through Polynesia, eastern Melanesia, and through Micronesia to the Ladrone (Marianas) Islands; and the third went from San Francisco to Panama, then to the Galápagos, then to Peru, then westward to Easter Island, back to the Galápagos, westward again to Mangareva (Gambier Islands), and then northward to Acapulco and San Diego. Although the *Albatross* was owned by the U.S. Fish Commission (USFC), the actual costs of these expeditions, not the least being the advance transport of coal to remote destinations, were covered by Agassiz.

All three *Albatross* cruises resulted in numerous publications on the systematics of the various organisms, mostly deep-sea, collected during the expeditions, as well as narrative volumes and descriptions of the coral-reef habitats by Agassiz himself (Agassiz, 1892, 1902, 1903, 1905, 1906). These publications, with their often sumptuous plates, appeared in the *Bulletin* and *Memoirs* of the MCZ, with the publication costs subsidized by Agassiz* through his fortunes derived from copper mines in Michigan.

Today these expeditions are best known by marine zoologists for their extensive discoveries of the deep-sea fauna, often from areas not well covered by previous expeditions, such as those of the *Challenger* in 1872–76. It is perhaps ironic that the Pacific and Indian Ocean expeditions of Agassiz were intended actually to allow him to collect data on the structure and formation of coral reefs in order to confirm his theories on this subject. Most zoologists are aware of the conclusions of

[1] Division of Mollusks NHB-118, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

* Agassiz (1912: 58) complained of the neglect by the U.S. government in not helping with the publication expenses.

Charles Darwin on the development of coral reefs, which today have received wide acceptance, albeit with some modifications. However, during the late 1800s there was not as strong a consensus concerning Darwin's views, with other hypotheses actively advanced by their proponents (Daly, 1916; Davis, 1928).

It will be recalled that Louis Agassiz [1807–73] was a vehement opponent of Darwin's theory of evolution by natural selection, so it is poignant to note that his son, Alexander, was to be just as opposed to Darwin's theory of coral-reef formation. That both father and son were wrong indicates their inflexible mentality (see also Winsor, 1991). In any case, the younger Agassiz, during his oceanographic cruises, certainly visited and studied far more coral reefs than had Darwin, James Dwight Dana (another key figure in this controversy), or indeed any other marine zoologist of those times. Yet Agassiz's approach to the coral-reef problem was strictly empirical: the accumulation of numerous observations that could, by inadequately explicated reasoning, be made to fit his own hypotheses.

Eventually, Darwin's views were confirmed for nearly all coral reefs, with Agassiz's hypotheses applying only to a few coral reefs that had formed on secondarily elevated platforms (as opposed to reefs around volcanic islands or barrier reefs). Indeed, Agassiz's voluminous research (1903) is scarcely if at all noted by modern historians of the coral-reef problem (e.g., Kühlmann, 1982; Stoddart, 1994), notwithstanding their doughty defenses in several hagiographic accounts of Agassiz's life (G. R. Agassiz, 1913; Mayer, 1910). In addition to studying the coral-reef problem, the *Albatross* expeditions were also intended to analyze the relationships of the deep-water fauna on either side of the Panamanian isthmus (Hedgpeth, 1945: 11; Wourms, 1992: 6) and the existence of the planktonic biota at intermediate oceanic depths (Mills, 1980); the former study was not completed by Agassiz, and the results of the latter study were disproven by other researchers.

Despite the fact that the primary rationale for Agassiz's Pacific and Indian Ocean expeditions has long since been rejected by marine zoologists, the specimens themselves and the systematic publications thereto remain of importance today in documenting the marine fauna of these regions.

For the Mollusca, the material from the *Albatross* expeditions of Agassiz was divided among several malacologists. The Cephalopoda of the first two expeditions were monographed by Hoyle (1904). The Nudibranchia and other shell-less Opisthobranchia of the first expedition were monographed by Bergh (1894). The discovery of a single specimen of *Dolabella* at Easter Island prompted an elaborate report on the "Dolabellinae" by MacFarland (1918) entailing a complete dissection of the holotype. The remaining shelled mollusks, as well as the brachiopods, were turned over to William Healey Dall [1845–1927] at the Smithsonian Institution (U.S. National Museum [USNM]). As Dall had previously treated the shelled mollusks of the *Blake* expeditions (Kabat, in press), Agassiz could confidently expect Dall to produce a work of similar quality on the *Albatross* Pacific material.

Dall's 1908 monograph on the shelled mollusks remains of fundamental importance in documenting and describing the (mostly) deep-sea biota of the eastern Pacific, along with a few taxa from Easter Island (Isla de Pascua) and nearby Isla Sala y Gómez. Many of these species are still known only from their original description and have not since been re-collected. Dall's monograph was largely based on the first and third *Albatross* cruises of Agassiz, together with some material from Mexico and southern California collected in 1888 by the *Albatross* during its earlier coastal surveys. The second *Albatross* cruise, which covered much of Polynesia and Micronesia, collected few benthic taxa (as the ocean floor in those regions was primarily

composed of manganese nodules), and only a small number of mollusk species were recorded by Dall.

The following two paragraphs are modified from Kabat (in press) concerning the *Blake* expedition mollusks, as the same principles and problems apply to the *Albatross* mollusks.

The majority of these species were based on several specimens, often coming from different stations, and holotypes were seldom specified by Dall in the original description. Although Dall often gave the USNM number for one lot under each species, he did not indicate the type status of that lot, and sometimes there were several specimens included in the lot. Numerous problems of interpretation of the type material by subsequent revisers have arisen over the past century. In the absence of a specified holotype, the presence of more than one specimen in the type material for a species means that these specimens are actually **syntypes** ["cotypes" in the older literature]. One specimen, usually the figured specimen, can be selected as the **lectotype** upon revision of the taxon. The remaining syntype(s) from the type lot(s) then automatically become **paralectotype(s)** (ICZN Articles 72–74).

Unfortunately, these principles concerning syntypes and lectotypes were often overlooked by malacologists in their taxonomic monographs. What frequently has occurred are statements that a given specimen (or lot) is the "holotype" and, sometimes, a statement that the remaining specimens are "paratypes." This, in fact, represents an inadvertent selection of a lectotype and paralectotypes by the subsequent author (ICZN Article 74).

Another problem concerning the *Albatross* material (as for that of the *Blake*) is that often the specimen lots were divided between the USNM (National Museum of Natural History, Smithsonian Institution) and the Museum of Comparative Zoology [MCZ] (Harvard University), although Dall did not explicitly note any MCZ records in his monograph. It is possible that the MCZ material was still at the Smithsonian at the time Dall's paper was completed. In researching the secondary literature, a lack of mention by authors of the MCZ material was noticed, sometimes with erroneous statements that the USNM specimen was the unique holotype when in fact syntypes were extant at the MCZ.

Also, as Kabat (in press) has discussed, during the Second World War the "type collections" of the USNM were stored at Luray in the Shenandoah Valley of central Virginia in order to protect them during possible bombing of the nation's capital. However, the haste necessitated by identifying and packing these specimens meant that no time could be devoted to researching their type status when they were removed from the general collection. After the war, at which time the type collection was kept separate, little curatorial attempt was made either to identify additional syntypes in the general collection or, indeed, to verify the type status of the material in the type collection itself. These problems are herein rectified, but they have assuredly led to confusion in the past as researchers often have assumed that a single specimen in the USNM type collection was per force the holotype.

One issue unique to the eastern Pacific marine mollusks in the USNM collection needs to be addressed as it too has caused problems. Several decades ago researchers with a special interest in this fauna undertook well-intentioned projects of carefully working through the USNM type collection, examining the type lots from the eastern Pacific, and then "recurating" those lots containing more than one specimen. In essence, what these researchers did was to determine which specimen (in a syntype series) was the "figured" or "measured" type, label that specimen as the "holotype" or "type," and then have the remaining syntype(s) *recataloged* under a new USNM number as "paratypes." The good intentions of these researchers to clarify taxonomic problems notwithstanding, these curatorial actions have no valid

standing under the ICZN for which only a published lectotype designation has standing. The relabeling of type material in this manner has no nomenclatural status and interferes with correct understanding of the actual type status of these syntypes. This author has identified numerous such "paratype" lots, some of which did indeed become paralectotypes in the subsequent literature, but most of which are really syntypes and have now been returned to the USNM type collection.

In contrast to the mollusks from the *Blake* publications, which had resulted in a vast subsequent literature containing numerous lectotype selections (the majority inadvertent), the mollusks from these *Albatross* expeditions have, as noted earlier, seldom been restudied, and most are still known only from the type material. Thus, the secondary literature is much smaller for this fauna.

There are, however, three publications that contain innumerable lectotype designations (nearly all inadvertent): Oldroyd's (1925–27) treatise on the marine mollusks of the northeastern Pacific and the two editions (1958, 1971) of Myra Keen's book on the marine mollusks of the tropical eastern Pacific. Although Oldroyd's treatise was judged to represent "essentially non-critical compilations of original descriptions . . ." (Coan and Kellogg, 1990: 175), she did include for many of Dall's species a statement that a certain lot was "Type" (albeit without further restriction). One of the major assets of Keen's books is that they include photographs of type specimens for many of the species treated. Few malacologists in recent years have noticed that in the back of these books, in the section titled "Sources of Illustrations," Keen (1958: 541–555; 1971: 935–966) provided not only the museum source of the figured specimen but also, for many type lots, the supposed type status.

It is obvious, however, that neither Oldroyd nor Keen researched the type status for the species described by Dall from the eastern Pacific. In many cases, Oldroyd or Keen cited a USNM specimen as "holotype" when in fact it was one of a syntype series. Therefore, their action constitutes a lectotype selection (ICZN Article 74) and has been so cited for numerous taxa in this catalog. This author has discussed these problems with several malacologists specializing in the eastern Pacific fauna. A review of the literature indicated that Jung (1989: 165) is the only source to have explicitly acknowledged this issue for a species described in Dall (1908). It is recommended that the curatorial staff of the museums whose type specimens were illustrated by Oldroyd or Keen, as well as researchers interested in the tropical eastern Pacific mollusk fauna, carefully check the relevant citations by Keen for other such inadvertent lectotype selections. Bieler (1993: 95) documented a similar problem for *Architectonica valenciennesii* Mörch, 1859.

An interesting point concerning Oldroyd's putative type statements is that our interpretation must be based on whether the USNM lot in fact had only one syntype specimen **at the time** of Oldroyd's publication. It will be recalled that in the 1950s–60s several researchers had "recataloged" certain USNM syntype lots. Suppose that a certain lot was one that Oldroyd had said to be "type"—today that lot might indeed contain only one specimen, but that might be a curatorial artifact of this subsequent recataloging process. If in Oldroyd's time that lot had instead comprised more than one specimen, then her "type" statement would not represent a valid lectotype selection.

It is obvious that the retroactive application of various ICZN provisions concerning the interpretation of type status to research or recuration done in good faith at the time represents a case of *ex post facto* judgment. One must consider that these researchers certainly could not have expected that their actions would be viewed in a different light by subsequent researchers following revised rules.

Note that despite the diverse technical

problems discussed here, there have been relatively few misinterpretations of taxa. This is ascribed to the general excellence of Dall's original descriptions and to the competence in discernment and interpretation of various subsequent authors.

One last point of some historical interest, which has not been noted in print previously, is brought out by a letter from Dall to Alexander Agassiz, dated October 10, 1896:

> Dear Professor, Yours of the 8th is at hand. . . . You may remember that there were two or three jars of the marines which did not turn up. A year or so later somebody sold some material in London which must have come from the *Albatross*, as I was informed by one of the London dealers; and I learned from Townsend that one of the employees [of the USFC] was suspected of stealing specimens, though it was not at the time capable of proof.°

The "London dealers" were presumably Sowerby & Fulton; one wonders whether or not any European conchologist was able to describe presumed new species from the stolen material or, indeed, whatever became of those specimens.

MATERIALS AND METHODS

The taxa described by Dall in his 1908 monograph were recorded and sorted into systematic sequence, by molluscan family. For each species, the citation to the original description is given, together with the type localities (mostly *Albatross* stations) as given by Dall. If Dall stated that a certain lot was "the type" (or similar wording), that is herein indicated. This listing was then carefully checked against the USNM type and general collections and the MCZ collection (in which types are housed together with the nontype material). Recognition of certain lots as types was facilitated by external evidence (ICZN Recommendation 72B). In addition, type specimens had been exchanged with S. S. Berry [1887–1984], a Californian malacologist who had a large private collection. The Berry collection is now in the Santa Barbara Museum of Natural History; Scott et al. (1990) documented the nongastropod types therein and P. H. Scott (email, July 19, 1995) kindly provided this author with a listing of the gastropod types described by Dall and now housed in that institution.

Also, researchers should be aware that later publications by Dall and various other authors have described new taxa from the three *Albatross* expeditions of Agassiz. In addition, the *Albatross* made numerous other cruises elsewhere in the northern Pacific (not sponsored by Agassiz) that have resulted in diverse systematic publications.

The 1908 report by Dall, in addition to comprising material from the three *Albatross* expeditions, also included specimens from various other collections, including several individual shell collectors. In the catalog, the name of these collectors, when given by Dall, is in all capitals, to distinguish it from the locality.

In some cases, it was not possible to find type material from all the stations as cited by Dall; either the specimens were lost or, more likely, they were subsequently reidentified as representing a different species, possibly in a different genus.

Dall (1908: 446–476) listed the *Albatross* dredging stations (3353–3437, 4567–4743) from the first and third expeditions; data from the earlier 1888 cruise can be found in Townsend (1901: 403ff.). For the reader's convenience, geographical data for those stations that represent type localities are given in the Appendix to this paper. Kabat (in press) discussed various problems concerning the localization of the *Blake* stations and the potential mixture of specimens and station data; these problems do not seem to have arisen for the *Albatross* material.

The subsequent literature on this fauna was checked for lectotype designations and illustrations of previously unfigured specimens, although as mentioned previously the two books of Keen (1958, 1971)

° Letter from Dall to Alexander Agassiz, October 10, 1896, MCZ Library Archives, bAg 241.10.1(100).

were the only major source of such citations. I have made no new lectotype designations herein, as such a task is best left for revisers of individual taxa.

This catalog was then re-sorted into a single alphabetical sequence by original binomen, with the current family name, as curated in the USNM collection, indicated for each species. There are inevitably some differences in the familial classification between the recently recurated collections of the USNM and the various older arrangements as used at the MCZ and other mollusk collections. For the reader's convenience, a Generic Index is placed at the end of this paper.

Abbreviations Used

ANSP	Academy of Natural Sciences of Philadelphia
CAS	California Academy of Sciences
DMNH	Delaware Museum of Natural History
fm	fathoms (1 fm = 6 feet = circa 1.83 meters)
MCZ	Museum of Comparative Zoology, Harvard University
SBMNH	Santa Barbara Museum of Natural History
USNM	U.S. National Museum (now the National Museum of Natural History, Smithsonian Institution)
	disarticulated (loose) valve (for the Bivalvia).

Note Regarding Types of Bivalvia

For the Bivalvia, many type lots consist of disarticulated (loose) valves. Specialists can best determine whether these valves represent matched pairs or different specimens. A further complication is that some bivalve families, notably the Propeamussiidae, have significant dimorphism in left/right valve size and/or sculpture. Unless otherwise specified, each bivalve lot has one specimen (= paired valves); others have either multiple specimens, or multiple loose valves, or a single valve.

CATALOG OF SPECIES-LEVEL TAXA

abbreviatus, Lepidopleurus halistreptus Dall, 1908: 354. *Albatross* 3417 [**7 syntypes, USNM 223498; 1 syntype, MCZ 27959; 3 syntypes, SBMNH 34461**]. Type material not mentioned by Ferreira (1979b: 153, 157). Leptochitonidae.

acrita, Leda (*Jupiteria*) Dall, 1908: 374–375. *Albatross* 2799 [**1 syntype, USNM 110690**; **numerous syntypes (100+ v), USNM 610320**; **syntypes (3 specimens + 5v), MCZ 27821**; **1 syntype, CAS 66509**; **syntypes (9 specimens + 4v), SBMNH 34057**]; *Albatross* 2794 [**1 syntype (1v), USNM 122761**]; *Albatross* 2801 [**1 syntype, USNM 96389**]; *Albatross* 2803 [**syntypes (11 specimens + 4v), USNM 96974**]. Nuculanidae.

agapea, Leda (*Jupiteria*) Dall, 1908: 373–374, plate 6, figures 4, 5. *Albatross* 3360 [**Lectotype, USNM 122911,** selected by Knudsen, as "the type" (1970: 26); **1 paralectotype, MCZ 27819**]; *Albatross* 3398 [**1 paralectotype (2v), USNM 122912**]. Nuculanidae.

agassizii, Borsonia (*Borsonella*) Dall, 1908: 275, plate 1, figure 5. *Albatross* 3361 [**Lectotype, USNM 123107,** selected by McLean in Keen, as "holotype" (1971: 959, caption to fig. 1759); **1 paralectotype, USNM 697375**]. Turridae.

agassizii, Cocculina Dall, 1908: 340. *Albatross* 4630 [**Holotype, USNM 110660** (figured by McLean in Keen, 1971: fig. 173)]. Cocculinidae.

agassizii, Solemya (*Acharax*) Dall, 1908: 365–366, plate 16, figure 10. *Albatross* 3360 [**Lectotype (2v), USNM 106885** (broken), selected by Oldroyd, as "Type" (1925: 10); **1 paralectotype (2v), MCZ 27814** (broken)]; *Albatross* 3381 [**paralectotypes (4v), USNM 106886** (broken); **1 paralectotype (2v), MCZ 27815** (broken)]; *Albatross* 3382 [**1 paralectotype (1v), USNM 122945** (broken); **1 paralectotype (2v), MCZ**

27816 (broken)]; *Albatross* 3399 [**not found**]; *Albatross* 3434 [**not found**]; *Albatross* 4654 [**1 paralectotype (1v), USNM** (uncataloged)]. The type material from *Albatross* 3399 and 3434 could not be found; possibly it was in the old USNM alcohol collection? Solemyidae.

agujana, Nucula Dall, 1908: 370, plate 10, figures 6, 7. *Albatross* 4654 [**syntypes (3 specimens + 4v), USNM 110571**; **1 syntype, MCZ 27808**]. Nuculidae.

agujanus, Polinices (*Euspira*) Dall, 1908: 334, plate 9, figure 2. *Albatross* 4643 [**Holotype, USNM 110566** (figured by Marincovich, 1977: 291–292, pl. 25, fig. 7)]. Naticidae.

altina, Pleurotomella (*Gymnobela*) *agonia* Dall var. Dall, 1908: 278–279, plate 14, figure 9. *Albatross* 3366 ("type") [**Holotype, USNM 123137**]. Dall also recorded this species from *Albatross* 3365 (even giving the number, USNM 123136), but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Turridae.

amabilis, Volutopsius "?" Dall, 1908: 305, plate 11, figure 9. *Albatross* 3392 [**Holotype, USNM 123008** (figured by Keen, 1971: fig. 1152)]. Buccinidae.

arciformis, Malletia (*Minormalletia*) Dall, 1908: 385–386, plate 15, figures 5, 6. *Albatross* 3417 [**2 syntypes, USNM 122926**; **1 syntype, MCZ 27833, 2v**]. Malletiidae.

armilda, Turris (*Surcula*) Dall, 1908: 262–263. *Albatross* 3017 [**1 syntype, USNM 110601; 2 syntypes, USNM 697380**]. Turridae.

atahualpa, Cylichnella (*Cylichnium*) Dall, 1908: 243, plate 11, figure 2. *Albatross* 3354 [**Holotype, USNM 123081**]. Cylichnidae.

atossa, Tindaria Dall, 1908: 388, plate 15, figures 3, 4. *Albatross* 3392 ("the type") [**Holotype, USNM 122920**]. Dall also recorded this species from *Albatross* 3393, but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Nuculanidae.

balaenorum, Terebra (*Strioterebrum*) Dall, 1908: 252. *Albatross* 2835 [**Lectotype, USNM 110599**, selected by Keen, as "holotype" (1958: 554, caption to fig. 957; see also Bratcher and Cernohorsky, 1987: 151, fig. 151b); **3 paralectotypes, USNM 610318**]; W. J. FISHER, La Paz, Gulf of California [**not found**]. Terebridae.

bathymetrae, Stilifer (*Mucronalia*) Dall, 1908: 318. On a species of *Bathymetra* [Crinoidea; = *Antedon*?], *Albatross* 3381. This specimen was not seen by Dall but was cited from Hartlaub (1895: 146–147, pl. 4, fig. 25), who stated "An dem Exemplar sitzt als Schmarotzer festgeheftet ein *Stylifer* verwandte Schneckenart (nach Prof. v. Martens wahrscheinlich eine *Mucronalia*)." Warén (1980: 199) stated "Type material lost. I consider this a *nomen dubium.*" Eulimidae.

benthima, Gemmula Dall, 1908: 267, plate 1, figure 7; plate 13, figure 4. *Albatross* 3392 [**Lectotype, USNM 123089**, selected by McLean in Keen, as "holotype" (1971: 958, caption to fig. 1650); **2 paralectotypes, USNM 537854; 1 paralectotype, MCZ 27894**]; *Albatross* 2807 [**3 paralectotypes, USNM 96485; 1 paralectotype, MCZ 27892**]; *Albatross* 3360 [**1 paralectotype, USNM 123087**]; *Albatross* 3365 [**1 paralectotype, USNM 123092**]; *Albatross* 3366 [**3 paralectotypes, USNM 123093; 2 paralectotypes, MCZ 27893**]; *Albatross* 3376 [**1 paralectotype, USNM 123088**]; *Albatross* 3413 [**1 paralectotype, USNM 123090**]. Turridae.

benthima, Malletia (*Minormalletia*) Dall, 1908: 386, plate 15, figures 1, 2. *Albatross* 3417 [**Holotype, USNM 122927**]. Malletiidae.

blanda, Daphnella (*Surculina*) Dall, 1908: 291, plate 3, figure 1. *Albatross* 3366 [**Holotype, USNM 123119**]. Turbinellidae.

borniana, Aligena Dall, 1908: 413, plate 10, figure 2. *Albatross* 4732 [**Holotype,**

USNM 110585 (figured by Harry, 1969: 176–177, figs. 30, 31)]. Kelliidae.

bridgesi, Terebra (*Strioterebrum*) Dall, 1908: 253. BRIDGES, Panama [**Lectotype, USNM 9404**, selected by Keen, as "holotype" (1971: 956, caption to fig. 1526, right; see also Bratcher and Cernohorsky, 1987: 144, pl. 42, figs. 162a, b); **7 paralectotypes, USNM 610319; 1 paralectotype, SBMNH 34779**]. Terebridae.

brunneopictum, Epitonium (*Ferminoscala*) Dall, 1908: 316–317, plate 8, figure 10. *Albatross* 2835 [**Holotype, USNM 97084** (figured by Keen, 1971: fig. 670)]. Epitoniidae.

calcar, Leda (*Spinula*) Dall 1908: 378, plate 10, figures 1, 10. *Albatross* 4658 [**1 syntype, USNM 110573** (broken) (as "type" in Knudsen, 1970: 39); **syntypes (2 specimens + 1v), USNM 683589** (broken); **1 syntype, MCZ 27825** (broken)]. Nuculanidae.

calcarella, Leda (*Spinula*) Dall, 1908: 378–379. *Albatross* 4656 [**1 syntype, USNM 110694**; **3 syntypes, USNM 110575** (**not found**)]. Nuculanidae.

calcipicta, Bursa (*Lampadopsis*) Dall, 1908: 320–321. *Albatross* 3368 [**Holotype, USNM 123027** (figured by Keen, 1958: fig. 328)]. Bursidae.

californica, Cancellaria (*Admete*?) Dall, 1908: 296–297, plate 4, figure 4. *Albatross* 2980 [**1 syntype, USNM 110626; 2 syntypes, USNM 635739**]; *Albatross* 3346 [**20+ syntypes, USNM 110624; 3 syntypes, MCZ 27928**]; *Albatross* 3194 [**2 syntypes, USNM 110625**]; *Albatross* 2839 [**1 syntype, USNM 122817**]; *Albatross* 2923 [**50+ syntypes, USNM 110627**]; *Albatross* 2936 [**3 syntypes, USNM 106823; 2 syntypes, USNM 110628**]; *Albatross* 4339 [**1 syntype, USNM 110629**]. Oldroyd (1927: 160) cited USNM 110626 as "Type," but this lot actually comprised more than one specimen at that time. Cancellariidae.

californica, Liotia (*Arene*) Dall, 1908: 344–345. *Albatross* 2984 [**1 syntype, USNM 110662; 5 syntypes, USNM 635457; 1 syntype, SBMNH 34780**]. Turbinidae.

californicus, Ptychatractus Dall, 1908: 299–300. *Albatross* 2923 [**1 syntype, USNM 193650; 1 syntype, USNM 635736**]. Turbinellidae.

callimene, Leda (*Jupiteria*) Dall, 1908: 372–373, plate 17, figures 3, 4. *Albatross* 3396 [**1 syntype, USNM 122910; numerous syntypes (30 + v), USNM 604252**; **syntypes (3v), MCZ 27818**; **1 syntype (1v), CAS 66408**; **syntypes (1 specimen + 1v), SBMNH 34058**]; Tome, Chile, in 14 fm [**numerous syntypes (20 + v), USNM 110689**]. Nuculanidae.

catallus, Alectrion (*Hima*) Dall, 1908: 307, plate 11, figure 11. *Albatross* 3355 [**Lectotype, USNM 123013**, selected by Keen, as "holotype" (1971: 954, caption to fig. 1292, left; see also Cernohorsky, 1975: 126–127, figs. 16, 17); **1 paralectotype, USNM 630936; 1 paralectotype, MCZ 27938**]. Nassariidae.

cetolaca, Mangilia Dall, 1908: 286. Replacement name for *Columbella* (*Aesopus*) *oldroydi* Arnold, 1903, non *Mangilia oldroydi* Arnold, 1903. Dall transferred *C.* (*A.*) *oldroydi* to the genus *Mangilia* at which it became a junior homonym. Turridae.

chilenica, Yoldia (*Yoldiella*) Dall, 1908: 380–381. *Albatross* 2781 [**2 syntypes, USNM 96923; syntypes (2 specimens + 8v), USNM 604253**; **1 syntype, MCZ 27837**]; *Albatross* 2782 [**syntypes (6v), USNM 96614**]. Nuculanidae.

chilensis, Capulus Dall, 1908: 329–330. *Albatross* 2781 [**1 syntype, USNM 96926; 1 syntype, USNM 678708**]. Capulidae.

chilensis, Poromya (*Dermatomya*) Dall, 1908: 430. *Albatross* 2785 [**Holotype, USNM 97135** (figured by Bernard, 1974: 90–91, pl. 25, figs. 1, 2)]. Poromyidae.

chrysocoma, Nucula Dall, 1908: 370–371, plate 18, figures 3, 4. *Albatross* 4656 [**syntypes (3 specimens + 2v), USNM**

110572; **1 syntype (2v), MCZ 27810**]; *Albatross* 2792 [**1 syntype (2v), USNM 122757**]; *Albatross* 3418 [**1 syntype, USNM 122899**]. Nuculidae.

chrysogona, Tellina (*Moerella*) Dall, 1908: 420–421, plate 10, figures 4, 8. *Albatross* 4642 [**syntypes (3v), USNM 110581**; **1 syntype (2v), MCZ 27855**]. Tellinidae.

citricus, Trophon (*Pascula*) Dall, 1908: 311–312. On the reefs at Easter Island [**Lectotype, USNM 110767**, selected by Rehder (1980: 74–75, pl. 9, fig. 11); **2 paralectotypes, USNM 633986**]. Muricidae.

clarinda, Pleurotomella (*Phymorhynchus*?) Dall, 1908: 285, plate 1, figure 3. *Albatross* 3381 [**Lectotype, USNM 123097**, selected by McLean in Keen, as "holotype" (1971: 961, caption to fig. 1863); **1 paralectotype, USNM 697423**]. Turridae.

clionella, Leucosyrinx "?" Dall, 1908: 270, plate 14, figure 3. *Albatross* 2792 ("types") [**4 syntypes, MCZ 27903; 2 syntypes, SBMNH 35488** (formerly USNM 97069)]. Dall also recorded this species from *Albatross* 3394, even providing the number USNM 123125 (which was cited as "holotype" by McLean in Keen, 1971: 958, caption to fig. 1666), but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Turridae.

cocosensis, Pecten (*Cyclopecten*) Dall, 1908: 405, plate 6, figures 1, 3. *Albatross* 3369 [**Lectotype, USNM 122870**, selected by Grau, as "holotype" (1959: 30–31, pl. 9, fig. 2); **1 paralectotype (2v), USNM 610126**; **1 paralectotype, MCZ 27852**]. Propeamussiidae.

colombiana, Nucula Dall, 1908: 371–372. *Albatross* 2799 [**1 syntype, USNM 110686; numerous syntypes (30 + v), USNM 619714** (figured by Olsson, 1961: 57, pl. 1, fig. 3); **3 syntypes, MCZ 27812**]; *Albatross* 2805 [**not found**]; *Albatross* 2792 [**1 syntype (2v), USNM 606808**]; *Albatross* 2784 [**1 syntype, USNM 122743**]; *Albatross* 2783 [**1 syntype (2v), USNM 96917**]. Nuculidae.

complicatus, Petaloconchus Dall, 1908: 326. *Albatross* 3368 [**numerous syntypes, USNM 123035**]. Both Oldroyd (1927: 654–655) and Keen (1958: 548, caption to fig. 199; 1971: 947, caption to fig. 495) have stated that USNM 123035 was the "type" or "holotype," but in fact this lot is an aggregate consisting of numerous tubes, each representing an individual specimen. A valid lectotype designation would necessitate the labeling of a single tube as the lectotype. Vermetidae.

compressa, Tindaria Dall, 1908: 387, plate 15, figures 7, 8; plate 17, figures 15, 16. *Albatross* 3360 [**1 syntype, USNM 122921** (broken) (as "type" in Knudsen, 1970: 56)]; *Albatross* 3414 [**2 syntypes, USNM 122923; 1 syntype (2v), MCZ 27826**]. Tindariidae.

constrictus, Polinices (*Euspira*) Dall, 1908: 337. *Albatross* 2780 [**Holotype, USNM 97065**]. Naticidae.

corbicula, Cancellaria (*Merica*) Dall, 1908: 294–295, plate 1, figure 4. *Albatross* 2936 [**4 syntypes, USNM 106878; 2 syntypes, USNM 206430; 2 syntypes, USNM 635740; 1 syntype, MCZ 27906**]; *Albatross* 4382 [**1 syntype, USNM 110620**]; *Albatross* 4407 [**1 syntype, USNM 110621**]; *Albatross* 4425 [**1 syntype, USNM 110662**]. Oldroyd (1927: 153) stated "Type in United States National Museum," but she did not restrict this to any one specimen. Cancellariidae.

cordyla, Leda (*Leda*) Dall, 1908: 375–376, plate 6, figures 6, 7. *Albatross* 3354 [**1 syntype, USNM 122915**]; *Albatross* 2792 [**syntype (2v), USNM 122755**]. Nuculanidae.

coronadoi, Borsonia (*Borsonella*) Dall, 1908: 277–278, plate 14, figure 2. *Albatross* 2931 [**Holotype, USNM 110608** (see also Oldroyd, 1927: 91)]. Turridae.

cortezi, Daphnella (*Surculina*) Dall, 1908: 292. *Albatross* 2919 [**Lectotype, USNM 110613**; selected by Oldroyd, as "Type"

(1927: 168–169)]; *Albatross* 4353 [**1 paralectotype, USNM 204050** (figured by Dall, 1925: 23, pl. 1, fig. 7)]. Turbinellidae.

crawfordianus, Polinices (*Euspira*) Dall, 1908: 335–336, plate 11, figure 7. *Albatross* 3356 [**Lectotype, USNM 123044**, selected by Marincovich, as "holotype" (1977: 292–293, pl. 25, fig. 9)]; *Albatross* 3407 [**not found**]; *Albatross* 3431 [**1 paralectotype, USNM 123051**]; *Albatross* 4654 [**1 paralectotype, USNM 110659**]; DR. CRAWFORD, southern Chile [**1 paralectotype, USNM 102586**]. Naticidae.

crebristriata, Irenosyrinx "?" Dall, 1908: 272–273, plate 13, figure 10. *Albatross* 2859 [**Holotype, USNM 122563** (see also Oldroyd, 1927: 68)]. Turridae.

cylindrellus, Scaphander Dall, 1908: 239, plate 8, figure 1. *Albatross* 4672 [**Holotype, USNM 110563**]. Cylichnidae.

decapitatus, Scaphander Dall, 1908: 240. *Albatross* 3683 [**Holotype, USNM 110746**]. Cylichnidae.

decenna, Drillia Dall, 1908: 265. *Albatross* 2798 [**Holotype, USNM 110603**]. Turridae.

delicata, Hipponix Dall, 1908: 331. *Albatross* 3355 [**Holotype, USNM 123041** (figured by Keen, 1971: fig. 764)]. Hipponicidae.

diazi, Limopsis Dall, 1908: 397, plate 18, figure 7. *Albatross* 3418 [**10 syntypes, USNM 122892; 1 syntype (2v), MCZ 27847**]. Limopsidae.

dicella, Yoldia (*Yoldiella*) Dall, 1908: 382. *Albatross* 3418 [**syntypes (4v), USNM 122917** (as "type lot" in Keen, 1971: 936, caption to fig. 61)]. Nuculanidae.

diegensis, Borsonia (*Borsonella*) Dall, 1908: 275–276, plate 13, figure 11. *Albatross* 2923 [**1 syntype, USNM 122573; 1 syntype, USNM 697372**]. Oldroyd (1927: 92) cited USNM 122573 as "Type," but this lot actually comprised more than one specimen at that time. Turridae.

diegensis, Limopsis Dall, 1908: 395, plate 15, figures 13, 15. F. W. KELSEY, off San Diego, 80 fm [**1 syntype, USNM 110699**]; *Albatross* 2923 [**syntypes (1 specimen + 2v), USNM 122585; numerous syntypes (20+ specimens), USNM 111422; 1 syntype, MCZ 27844; numerous syntypes (20+ specimens), MCZ 187523; syntypes, ANSP 190954; syntypes (1 specimen + 2v), DMNH 20487; 4 syntypes, DMNH 43614; 5 syntypes, SBMNH 34060**]. Oldroyd (1925: 44) cited USNM 122585 as "Type," but this lot actually comprises more than one specimen. Limopsidae.

dinora, Pleurotomella (*Pleurotomella*) Dall, 1908: 281. *Albatross* 2807 [**Holotype, USNM 96479** (figured by McLean in Keen, 1971: fig. 1856)]. Turridae.

diomedae, Cocculina Dall, 1908: 341, plate 16, figures 4, 7. *Albatross* 3393 [**Holotype, USNM 123052**]. Cocculinidae.

diomedae, Lima (*Acesta*) Dall, 1908: 407–408, plate 7, figure 2. *Albatross* 3404 [**Holotype, USNM 122875**]. Limidae.

diomedaeus, Murex (*Tritonalia*) Dall, 1908: 313–314, plate 12, figures 4, 5. *Albatross* 3397 [**Holotype, USNM 123020** (figured by Keen, 1971: fig. 985, upper)]. Muricidae.

dolenta, Turris (*Surcula*) Dall, 1908: 262. *Albatross* 2804 ("type") [**Holotype, USNM 96645** (figured by Keen, 1958: fig. 902)]. Dall also recorded this species from *Albatross* 3389, but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Turridae.

donacia, Vesicomya Dall, 1908: 417, plate 17, figures 9, 13. *Albatross* 3392 [**Holotype (1v), USNM 122929**]. Vesicomyidae.

dotella, Turris (*Surcula*) Dall, 1908: 263–264. *Albatross* 2823 [**Holotype, USNM 96731** (figured by Keen, 1958: fig. 842)]. Turridae.

edentula, Strombina Dall, 1908: 310–311. *Albatross* 2830 [**Lectotype, USNM 96578**, selected by Keen, as "holotype" (1971: 954, caption to fig. 1286; see also

Jung, 1989: 165–170, figs. 216–1–216–6), **1 paralectotype, USNM 859116**]. Columbellidae.

egregia, Pleurotomella (*Gymnobela*) Dall, 1908: 279. *Albatross* 4656 [**Holotype, USNM 110610** (figured by McLean in Keen, 1971: fig. 1851)]. Turridae.

eldorana, Gemmula Dall, 1908: 268, plate 14, figure 8. *Albatross* 3392 [**Lectotype, USNM 123120**, selected by McLean in Keen, as "holotype" (1971: 958, caption to fig. 1651); **1 paralectotype, USNM 537856; 1 paralectotype, MCZ 27897**]; *Albatross* 2807 [**1 paralectotype, USNM 96491; 1 paralectotype, USNM 537587**]. Turridae.

elegans, Solenosteira Dall, 1908: 300–301, plate 5, figure 6. *Albatross* 3355 [**5 syntypes, USNM 123003; 1 syntype, SBMNH 34667**]. A junior secondary homonym of *Cantharus elegans* Gray in Griffith and Pidgeon, 1834; renamed *Cantharus rehderi* Berry, 1962 (page 130). Buccinidae.

elevata, Oocorys Dall, 1908: 322–323, plate 8, figure 9. *Albatross* 4649 [**Holotype, USNM 110569**]. Cassidae.

encella, Mangilia Dall, 1908: 287–288, plate 14, figure 11. *Albatross* 3366 [**Lectotype, USNM 123113**, selected by McLean in Keen, as "holotype" (1971: 961, caption to fig. 1852); **1 paralectotype, USNM 697376**]. Turridae.

endemica, Arca (*Cucullaria*) Dall, 1908: 399, plate 17, figure 8. *Albatross* 4721 [**1 syntype, USNM 110578**]; *Albatross* 4685 [**1 syntype, USNM 110707**]. Arcidae.

enora, Mangilia Dall, 1908: 286, plate 4, figure 6. *Albatross* 3376 [**Holotype, USNM 123121** (figured by McLean in Keen, 1971: fig. 1857)]. Turridae.

equatorialis, Poromya (*Dermatomya*) Dall, 1908: 429–430, plate 5, figures 1, 2. *Albatross* 3360 [**Lectotype (2v), USNM 122942**; selected by Bernard, as "holotype" (1974: 91–92, pl. 22, figs. 2–4)]; *Albatross* 2793 [**1 paralectotype (2v), MCZ 27859**]. Poromyidae.

equatorialis, Solariella Dall, 1908: 351–352, plate 5, figure 11. *Albatross* 3376 [**Lectotype, USNM 122964** ("125964"), selected by McLean in Keen, as "holotype" (1971: 944, caption to fig. 65); **4 paralectotypes, USNM 635471; 1 paralectotype, MCZ 27955; 1 paralectotype, SBMNH 34776**]; *Albatross* 3375 [**2 paralectotypes, USNM 122963**]; *Albatross* 3366 [**2 paralectotypes, USNM 122962**]. Oldroyd (1927: 796–797) cited USNM "125964" [= 122964] as "Type," but this lot actually comprised more than one specimen at that time; much later it was recurated into two lots, allowing for McLean's lectotype selection. Trochidae.

erosina, Leucosyrinx Dall, 1908: 269, plate 2, figure 1. *Albatross* 3360 [**Lectotype, USNM 123106**, selected by McLean in Keen, as "holotype" (1971: 960, caption to fig. 1763); **2 paralectotypes, USNM 697374; 2 paralectotypes, MCZ 27902**]. Turridae.

esilda, Pleurotomella (*Pleurotomella*) Dall, 1908: 282. *Albatross* 3395 [**Holotype, USNM 123126** (figured by McLean in Keen, 1971: fig. 1668)]. Turridae.

estuarinus, Acteon (*Microglyphis*) Dall, 1908: 238. *Albatross* 3194 [**Lectotype, USNM 110598**, selected by Keen, as "holotype" (1971: 962, caption to fig. 2232); **2 paralectotypes, USNM 678736**]. Oldroyd (1927: 27) stated "Type in the United States National Museum" without specifying a lot or specimen; at that time, USNM 110598 actually comprised three syntypes. Acteonidae.

esuriens, Gemmula Dall, 1908: 265–266. *Albatross* 3392 [**1 syntype, USNM 123128**]; *Albatross* 3407 [**1 syntype, MCZ 27895** (formerly USNM 123129)]. Turridae.

exopleura, Cancellaria (*Narona*) Dall, 1908: 294. *Albatross* 2804 [**Lectotype, USNM 96638**, selected by Keen, as "holotype" (1958: 552, caption to fig. 701); **1 paralectotype, MCZ 27926**]; DR. JONES, Payta, Peru [**1 paralectotype, USNM 46286**]. Cancellariidae.

exsarcus, Alectrion (*Tritia*) Dall, 1908: 308, plate 11, figure 12. *Albatross* 4642 [**Holotype, USNM 110565** (figured by Keen, 1971: fig. 1297; see also Cernohorsky, 1975: 146, figs. 52, 53)]. Nassariidae.

ferminianum, Epitonium (*Ferminoscala*) Dall, 1908: 316, plate 8, figure 8. *Albatross* 2834 ("figured type") [**Holotype, USNM 96818**]. Dall also recorded this species from *Albatross* 2804, 3391, and 3034, but such records are excluded from the type series. Epitoniidae.

fluctigera, Tellina (*Phyllodina*) Dall, 1908: 419–420. *Albatross* 3355 [**Holotype (1v), USNM 122935** (figured by Keen, 1958: fig. 407; 1971: fig. 545)]. Tellinidae.

fragillissimus, Fusinus Dall, 1908: 301–302, plate 12, figure 6. *Albatross* 3398 [**Holotype, USNM 123007** (figured by Keen, 1971: fig. 1347)]. Transferred from Fasciolariidae to Buccinidae by Olsson (1971: 57–58, figs. 12, 24, 25). Buccinidae.

fusidens, Columbella (*Anachis*) Dall, 1908: 309, plate 11, figure 13. *Albatross* 4642 [**1 syntype, USNM 110616; 1 syntype, USNM 678719; 1 syntype, MCZ 27944**]. Columbellidae.

fusinella, Turris (*Surcula*) Dall, 1908: 261–262, plate 14, figure 7. *Albatross* 3391 [**1 syntype, USNM 123086**]; *Albatross* 3017 [**1 syntype, USNM 110600; 1 syntype, MCZ 27900**]. Turridae.

galapagana, Solariella Dall, 1908: 350–351, plate 4, figure 2. *Albatross* 3413 [**Holotype, USNM 122959** (figured by McLean in Keen, 1971: fig. 66)]. Trochidae.

garretti, Myonera Dall, 1908: 434–435, plate 5, figure 4. *Albatross* 3380 [**Holotype, USNM 122941** (figured by Bernard, 1974: 70–71, pl. 19, fig. 1)]. Cuspidariidae.

genilda, Mangilia "?" Dall, 1908: 286–287, plate 13, figure 3. *Albatross* 3392 [**1 paralectotype, USNM 123131**]; *Albatross* 3393 [**Lectotype, USNM 123132**, selected by McLean in Keen, as "holotype" (1971: 958, caption to fig. 1644); **2 paralectotypes, USNM 517974; 1 paralectotype, MCZ 27910**]. Turridae.

goniopleura, Alectrion (*Tritia*?) Dall, 1908: 308–309. *Albatross* 4641 [**Holotype, USNM 110630** (figured by Keen, 1971: fig. 1301)]. Nassariidae.

granula, Yoldia (*Yoldiella*) Dall, 1908: 382. *Albatross* 2778 [**Holotype, USNM 110693**]. Nuculanidae.

herilda, Gemmula Dall, 1908: 266–267. *Albatross* 3360 [**Holotype, USNM 123091** (figured by McLean in Keen, 1971: fig. 1670; however, the catalogue number is given on page 958 as USNM 123130, which is actually that of the following species in the book, *monochorda*)]. Turridae.

hesperus, Macoma (*Psammacoma*) Dall, 1908: 421–422. *Albatross* 3355 ["2355"] [**Holotype (1v), USNM 122936** (figured by Keen, 1971: fig. 564)]. Tellinidae.

hupeana, Macoma Dall, 1908: 421. Replacement name for *Tellina inornata* Hupé in Gay, 1854, non Hanley, 1844. Tellinidae.

immaculata, Glyphostoma Dall, 1908: 289–290. plate 1, figure 9. *Albatross* 3391 [**Lectotype, USNM 123115**, selected by McLean in Keen, as "holotype" (1971: 960, caption to fig. 1786); **1 paralectotype, USNM 697378**]. Turridae.

imparella, Daphnella (*Eubela*) Dall, 1908: 291, plate 2, figure 2. *Albatross* 3392 [**Lectotype, USNM 123114**, selected by McLean in Keen, as "holotype" (1971: 961, caption to fig. 1853); **7 paralectotypes, USNM 697377; 2 paralectotypes, MCZ 27924**]. Turridae.

inca, Cylichnella (*Bullinella*) Dall, 1908: 242, plate 11, figure 3. *Albatross* 3392 [**Holotype, USNM 123080**]. Cylichnidae.

incongruus, Lepidopleurus Dall, 1908: 355. *Albatross* 3354 [**Lectotype, USNM 122969**, selected by Ferreira, as "holotype" (1979b: 157–158, fig. 29; see

also Kaas and van Belle, 1985: 88–89, figs. 1–8); **1 paralectotype, MCZ 27957** (overlooked by Ferreira, 1979b)]. Leptochitonidae.

indolens, Yoldie [sic = *Yoldia*] (*Yoldiella*) Dall, 1908: 381. *Albatross* 2784 [**syntypes (20 + v), USNM 122740**; **syntypes (1 specimen + 2v), MCZ 27838**]; *Albatross* 2785 [**syntypes (5 specimens + 9v), USNM 96908**]. Nuculanidae.

inequalis, Malletia Dall, 1908: 383–384. *Albatross* 2772 [**syntype (2v), USNM 193350**]; *Albatross* 2778 [**1 syntype (1v), USNM 193349**]. Malletiidae.

infrequens, Yoldia (*Yoldiella*?) Dall, 1908: 381. *Albatross* 2784 [**1 syntype (1v), USNM 110692**]; *Albatross* 2783 [**1 syntype, USNM 96908**]. Nuculanidae.

ira, Corbula (*Cuneocorbula*) Dall, 1908: 423. *Albatross* 3355 [**syntypes (3v), USNM 122944** (as "holotype" in Keen, 1971: 943, caption to fig. 687, but all three valves were figured!)]. Corbulidae.

isogonia, Pleurotomella (*Gymnobela*) Dall, 1908: 279–280, plate 4, figure 3. *Albatross* 3393 [**Holotype, USNM 123112** (figured by McLean in Keen, 1971: fig. 1866)]. Turridae.

juarezi, Limopsis Dall, 1908: 396, plate 18, figure 8. *Albatross* 3360 [**syntypes (4 specimens + 6v), USNM 122891**; **1 syntype, MCZ 27846; 1 syntype, SBMNH 34680**]; *Albatross* 3418 [**1 syntype, USNM 110559**]. Limopsidae.

leonilda, Yoldia (*Yoldiella*) Dall, 1908: 382–383. *Albatross* 3360 [**Holotype, USNM 122909** (broken)]. Nuculanidae.

leonis, Irenosyrinx persimilis Dall var.? Dall, 1908: 272. *Albatross* 3074 [**1 syntype, USNM 110605; 1 syntype, USNM 697418; 1 syntype, MCZ 27919**]. Oldroyd (1927: 66) cited USNM 110605 as "Type," but this lot actually comprised more than one specimen at that time. Turridae.

liriope, Pecten (*Pseudamusium*) Dall, 1908: 402. *Albatross* 3392 [**Lectotype, USNM 122869**, selected by Grau as "holotype" (1959: 27–28, pl. 8, fig. 1; see also Keen, 1971: fig. 189); **1 paralectotype (2v), USNM 609941**; **1 paralectotype, MCZ 27850**]. Propeamussiidae.

litorinus, Polinices (*Euspira*) Dall, 1908: 337–338. *Albatross* 2807 [**Lectotype, USNM 96481**, selected by Marincovich, as "holotype" (1977: 293–294, pl. 25, fig. 10); **4 paralectotypes, USNM 678712; 2 paralectotypes, MCZ 27948**]. Marincovich (1977: 294) incorrectly stated that this species was ". . . known from a single specimen . . ."; in fact, six other type specimens are extant. Naticidae.

lobula, Leda (*Jupiteria*) Dall, 1908: 375. *Albatross* 3422 [**Holotype, USNM 122918** (figured by Keen, 1958: fig. 21)]. Nuculanidae.

loshka, Leda (*Leda*) Dall, 1908: 376, plate 17, figure 2. *Albatross* 3392 [**2 syntypes, USNM 122916; 1 syntype (2v), MCZ 27823**]. Nuculanidae.

lucana, Terebra (*Strioterebrum*) Dall, 1908: 252–253. *Albatross* 2830 [**Lectotype, USNM 96567**, selected by Keen, as "holotype" (1971: 956, caption to fig. 1548, left; see also Bratcher and Cernohorsky, 1987: 134, pl. 38, fig. 149a); **6 paralectotypes, USNM 610317; 1 paralectotype, SBMNH 34778**]. Terebridae.

mabillei, Rochefortia Dall, 1908: 413–414. *Albatross* 2778 [**syntypes (4v), USNM 110714**]. Leptonidae.

mabilliana, Limopsis Dall, 1908: 395–396. *Albatross* 2780 [**Holotype, USNM 110703**]. Limopsidae.

magellanicus, Corneocyclas Dall, 1908: 411. *Albatross* 2778, "a single right valve evidently washed into the sea from some stream" [**Holotype (1v), USNM 110712**]. Sphaeriidae.

malpelonium, Amusium (*Propeamusium*) Dall, 1908: 405–406, plate 6, figure 9. *Albatross* 3360 [**syntypes (7 specimens + 9v), USNM 122871**]; *Albatross* 3374 [**numerous syntypes (20+ specimens), USNM 122873**]; *Albatross*

3381 [**6 syntypes, USNM 122874**]; *Albatross* 3361 [**syntypes (8 specimens + 9v), USNM 122872**]; *Albatross* 3684 [**not found**]. Grau (1959: 14, pl. 2, fig. 1) referred to "Holotype: U.S. National Museum. Type locality: *Albatross* station 3360 . . . ." However, Grau did not specify which of numerous specimens from USNM 122871 (*Albatross* 3360) was the "holotype" (i.e., the lectotype), and the figured specimen is actually from *Albatross* 3374 (captioned by Grau as a "paratype"). Knudsen (1970: 96) also referred to "the type from *Albatross* St. 3360" but again did not specify a lectotype. Propeamussiidae.

mantana, Yoldia (*Yoldiella*?) Dall, 1908: 381–382. *Albatross* 2792 [**Holotype, USNM 122756** (figured by Keen, 1971: fig. 63)]. Nuculanidae.

mariana, Turritella Dall, 1908: 327, plate 11, figure 14. *Albatross* 3427 [**Holotype, USNM 123036** (see also Oldroyd, 1927: 656–657)]. Turritellidae.

mazatlanicus, Acteon (*Microglyphis*) Dall, 1908: 237, plate 5, figure 7. *Albatross* 3431 [**Holotype, USNM 123075**]. Acteonidae.

mexicana, Tindaria Dall, 1908: 389, plate 17, figures 11, 14. *Albatross* 3418 [**Holotype, USNM 122925** (see also Oldroyd, 1925: 40–41)]. Nuculanidae.

mexicana, Xylophaga Dall, 1908: 425. *Albatross* 3422 ("two right valves") [**Lectotype (1v), USNM 122947**, selected by Turner, as "holotype" (1955: 150–151, pl. 90); **1 paralectotype (1v), USNM 887577**]. Oldroyd (1925: 215) stated "Type in U.S.N.M.," but she did not indicate the lot or specimen. Pholadidae.

microsoma, Cancellaria (*Merica*?) Dall, 1908: 296, plate 11, figure 10. *Albatross* 3418 [**Lectotype, USNM 122997,** selected by Oldroyd, as "Type" (1927: 157); **1 paralectotype, MCZ 27927**]. Cancellariidae.

minuscula, Pholadidea (*Penitella*) Dall, 1908: 425. *Albatross* 3392 [**syntypes (1 specimen + 3v + 2 mesoplaxes), USNM 122946**]. Turner (1955: 113, pl. 66, fig. 1) stated that USNM 122946 was the "holotype," but she did not specify which of the syntypes was the holotype. Turner's figure is of the mesoplax of the "holotype," but this is not sufficient to determine the holotype itself. Pholadidae.

miser, Alectrion (*Hima*) Dall, 1908: 307–308, plate 4, figure 1. *Albatross* 3355 [**1 syntype, USNM 123014; 2 syntypes, USNM 678729; 1 syntype, MCZ 27939**]; *Albatross* 3354 [**9 syntypes, USNM 123012; 2 syntypes, MCZ 27940; 1 syntype, SBMNH 34775**]; *Albatross* 3387 [**1 syntype, USNM 123015**]; *Albatross* 3389 [**1 syntype, USNM 106894**]; *Albatross* 3391 [**1 syntype, USNM 123016**]; *Albatross* 3396 [**8 syntypes, USNM 123017**]; *Albatross* 3422 [**1 syntype, USNM 123018**]. Nassariidae.

miser, Pecten (*Pallium*) Dall, 1908: 401, plate 8, figure 6. *Albatross* 3355 ("two upper valves") [**1 syntype (1v), USNM 122862**; **1 syntype (1v), MCZ 27849**]. Pectinidae.

monochorda, Clinura Dall, 1908: 292–293, plate 13, figure 1. *Albatross* 3393 [**Holotype, USNM 123130** (figured by McLean in Keen, 1971: fig. 1671)]. Turridae.

mörchii, Troschelia (*Thalassoplanes*) Dall, 1908: 303–304. *Albatross* 3684 [**Holotype, USNM 110750**]. Buccinidae.

morgana, Bullaria (*Leucophysema*) Dall, 1908: 244, plate 11, figure 4. *Albatross* 3392 [**1 syntype, USNM 123082; 1 syntype, MCZ 27920**]. Bullidae.

movilla, Mangilia Dall, 1908: 285–286, plate 14, figure 6. *Albatross* 3418 [**Lectotype, USNM 123118**, selected by McLean in Keen, as "holotype" (1971: 958, caption to fig. 1672); **1 paralectotype, MCZ 27911**]. Turridae.

nassa, Cocculina Dall, 1908: 341, plate 16, figures 3, 6. *Albatross* 3392 [**1 syntype, USNM 123053; 4 syntypes, USNM 678688; 1 syntype, MCZ 27905; 1**

syntype, SBMNH 34781]. Cocculinidae.

neoceanicus, Pecten (*Pseudamusium*) Dall, 1908: 402–403, plate 9, figure 4. *Albatross* 4721 [**Holotype, USNM 110579** (figured by Grau, 1959: 56–57, pl. 2, fig. 2)]. Pectinidae.

nesiotes, Thais Dall, 1908: 311. Easter Island (shore) [**Lectotype, USNM 110766**, selected by Rehder, as "holotype" (1980: 73–74); **2 paralectotypes, USNM 633987**]. Thaididae.

notilla, Turris (*Surcula*) Dall, 1908: 263. *Albatross* 3017 [**Holotype, USNM 110602** (figured by Keen, 1958: fig. 906)]. Turridae.

nucleator, Arca (*Bathyarca*) Dall, 1908: 397–398, plate 18, figure 9. *Albatross* 3392 [**syntypes, USNM 122876 (1 specimen + 1v); 1 syntype, MCZ 27848**]. Oldroyd (1925: 46) cited USNM 122876 as "Type," but this lot actually comprises more than one specimen. Arcidae.

occidentalis, Cavolina Dall, 1908: 233, pl. 12, figs. 1, 1b, 1c. Type locality not given [**1 syntype, USNM 110591; 5 syntypes, USNM 734213** (both lots from North Pacific Ocean, 38°N, 137°W) (see also Spoel, 1967: 95)]. Cavoliniidae.

occidentalis, Seguenzia Dall, 1908: 325. *Albatross* 3418 [**Lectotype, USNM 123033**, selected by McLean in Keen, as "holotype" (1971: 945, caption to fig. 177); **1 paralectotype, MCZ 27941**]. Seguenziidae.

oceanica, Pleurotomella (*Phymorhynchus*) Dall, 1908: 284–285. *Albatross* 3681 [**Holotype, USNM 110751**]. Turridae.

opacus, Lepidopleurus Dall, 1908: 354–355. *Albatross* 4647 [**Lectotype, USNM 110664**, selected by Smith and Ferreira, as "holotype" (1977: 84, fig. 3; see also Ferreira, 1979b: 153, 154); **1 paralectotype, USNM 887578** (disarticulated; figured in Smith and Ferreira, 1977: fig. 4); **1 paralectotype, SBMNH 34460**]; *Albatross* 3392 [**1 paralectotype, USNM 122970; 2 paralectotypes, USNM 122972; 1 paralectotype, MCZ 27960**]. Leptochitonidae.

ophioderma, Ischnochiton Dall, 1908: 356. On the shore at Perico Island, Panama Bay [**Lectotype, USNM 110764**, selected by Smith (1977: 229); **1 paralectotype, USNM 880053**]. A senior homonym and a senior synonym of *Ischnochiton ophioderma* Dall, 1919 (see also Baker, 1937). Ischnochitonidae.

orariana, Clathurella Dall, 1908: 288, plate 14, figure 12. *Albatross* 3392 [**Holotype, USNM 123117** (figured by McLean in Keen, 1971: fig. 1859)]. *Pleurotomella oceanida* Dall, 1919 is based on the same type specimen (fide McLean in Keen, 1971: 764). Turridae.

othello, Natica (*Cochlis*) Dall, 1908: 332–333. STEARNS, Panama ("types") [**Lectotype, USNM 46446**, selected by Marincovich, as "holotype" (1977: 377–379, pl. 37, fig. 1), **2 paralectotypes, USNM 678715**]. Dall also recorded this species from *Albatross* 2799, 2800, 2801, 2803, 2804, 3354, and 3392, but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Naticidae.

pacifica, Cerithioderma Dall, 1908: 324–325. *Albatross* 3392 [**Lectotype, USNM 123032**, selected by Warén and Bouchet (1986: 161–162, figs. 4, 17; also figured by Keen, 1971: fig. 836); **1 paralectotype, USNM 887576**]. Provannidae.

pacifica, Leucosyrinx "?" Dall, 1908: 270–271, plate 12, figure 3. *Albatross* 2859 [**Holotype, USNM 122590** (see also Oldroyd, 1927: 67)]. Buccinidae.

pacifica, Lyonsiella Dall, 1908: 428. *Albatross* 4693 [**Holotype, USNM 110583** (figured by Bernard, 1974: 111–112, pl. 28, figs. 1, 2)]. Verticordiidae.

pacificum, Bathysciadium Dall, 1908: 339–340, plate 9, figures 1, 3, 7. *Albatross* 4656 [**1 syntype, USNM 110570; 1 syntype, USNM 678690**]. Bathysciadiidae.

pacis, Liotia (*Arene*) Dall, 1908: 345. *Albatross* 2996 [**Lectotype, USNM**

110663, selected by McLean in Keen, as "holotype" (1971: 945, caption to fig. 136); **1 paralectotype, USNM 635451**]. Turbinidae.

panamella, Clathurella Dall, 1908: 288–289, plate 14, figure 1. *Albatross* 3391 [**1 syntype, USNM 123104**]; *Albatross* 2804 [**6 syntypes, USNM 122771**]. Turridae.

panamense, Dentalium megathyris Dall, 1908: 358. *Albatross* 3360 [**1 syntype, USNM 122982**]; *Albatross* 3361 [**7 syntypes, USNM 122977; 1 syntype, USNM 594263; 1 syntype, SBMNH 35019**]; *Albatross* 3381 [**16 syntypes, USNM 122975; 3 syntypes, MCZ 27967** (broken)]. Dentaliidae.

panamensis, Acteon Dall, 1908: 236–237, plate 11, figure 6. *Albatross* 3392 [**Holotype, USNM 123074**]. Acteonidae.

panamensis, Cuspidaria Dall, 1908: 432, plate 16, figure 2. *Albatross* 3394 [**Holotype, USNM 122937** (see also Bernard, 1974: 40–41, pl. 13, figs. 5, 6)]. Cuspidariidae.

panamensis, Fusinus Dall, 1908: 301. *Albatross* 3391 [**Holotype, USNM 123004**]. Fasciolariidae.

panamensis, Leptothyra Dall, 1908: 342–343, plate 5, figure 9. *Albatross* 3358 [**Holotype, USNM 123055** (figured by McLean in Keen, 1971: fig. 140)]. Turbinidae.

panamensis, Lyonsia Dall, 1908: 427, plate 18, figure 12. *Albatross* 4630 [**Holotype (1v), USNM 110584**]. Lyonsiidae.

panamensis, Pecten (*Pseudamusium*) Dall, 1908: 404, plate 6, figures 8, 10. *Albatross* 3354 [**syntypes (9v), USNM 122865**; **syntypes (4v), MCZ 27851**]; *Albatross* 3389 [**numerous syntypes (20 + v), USNM 106895**]; *Albatross* 3396 [**syntypes (16v), USNM 122866**]; *Albatross* 3407 [**1 syntype (1v), USNM 122867**]; *Albatross* 3422 [**1 syntype, USNM 122868**]. A junior homonym (non Dall, 1898); renamed *Pecten* (*Delectopecten*) *zacae* Hertlein, 1935 (pages 321–322). However, Hertlein used his own specimens (in the CAS) as the "holotype" and "paratypes" of *zacae*, which is incorrect, as the type material remains that of the original name! Grau (1959: 51) stated "Holotype: U.S. National Museum," but the exact lot was not specified. Pectinidae.

panamensis, Protocardia Dall, 1908: 415, plate 18, figure 1. *Albatross* 3355 [**Lectotype, USNM 122928**, selected by Olsson, as "holotype" (1961: 254, pl. 39, fig. 4); **paralectotypes (3 specimens + 10v), USNM 609954**; **paralectotypes (1 specimen + 2v), MCZ 27862**; **1 paralectotype, CAS 64429**]. Cardiidae.

panamensis, Solemya (*Petrasma*) Dall, 1908: 366. *Albatross* 2799 [**Lectotype, USNM 110678** (broken), selected by Oldroyd, as "Type" (1925: 11; see also Keen, 1958: 547, caption to fig. 605)]; *Albatross* 2973 [**1 paralectotype, USNM 110679 (not found)**]. Although Oldroyd cited "110679," the station given by her was 2799 and her catalog number appears to be a typographical error. Solemyidae.

panamensis, Terebra (*Strioterebrum*) Dall, 1908: 250–251, plate 5, figure 10. *Albatross* 3391 ["3291"] [**Lectotype, USNM 123084**, selected by Keen, as "holotype" (1971: 957, caption to fig. 1555, right; see also Bratcher and Cernohorsky, 1987: 148, 150, pl. 44, figs. 168a–c); **5 paralectotypes, USNM 678732; 1 paralectotype, SBMNH 34777**]; *Albatross* 2834 [**1 paralectotype, USNM 96714**]. Terebridae.

panamensis, Tindaria Dall, 1908: 388, plate 17, figures 10, 12. *Albatross* 3392 [**syntypes (3 specimens + 4v), USNM 122922**; **1 syntype (2v), MCZ 27827**]. Tindariidae.

panamensis, Yoldia (*Orthoyoldia*) Dall, 1908: 380. *Albatross* 3354 [**Lectotype, USNM 122900**, selected by Keen, as "holotype" (1971: 936, caption to fig. 59); **1 paralectotype, MCZ 27836**]; *Albatross* 3355 [**1 paralectotype (2v), USNM 122901** (broken)]. Nuculanidae.

panamina, Nucula Dall, 1908: 368, plate 6, figure 11. *Albatross* 3360 [**syntypes (3 specimens + 4v), USNM 122894** (as "type" in Knudsen, 1970: 19)]. Nuculidae.

pardoanus, Polinices (*Euspira*) Dall, 1908: 336. *Albatross* 3361 [**Lectotype, USNM 123046**, selected by Keen, as "holotype" (1971: 950, caption to fig. 887; see also Marincovich, 1977: 294–295, pl. 25, fig. 11)]; *Albatross* 3407 [**1 paralectotype, USNM 123050**]; *Albatross* 3366 [**1 paralectotype, USNM 123047**]. Naticidae.

parella, Pleurotomella (*Pleurotomella*) Dall, 1908: 282–283, plate 14, figure 4. *Albatross* 3376 [**Holotype, USNM 123135** (figured by McLean in Keen, 1971: fig. 1860)]. Turridae.

pasca, Pecten (*Chalmys*) [sic = *Chlamys*] Dall, 1908: 401–402. Easter Island (beach) [**Holotype (1v), USNM 110765** (figured by Rehder, 1980: 109, pl. 13, fig. 6)]. Pectinidae.

patagonicus, Phaseolus (*Silicula*) Dall, 1908: 392. *Albatross* 2783 [**Holotype (1v), USNM 96914**]. Phaseolidae.

pedroana, Terebra (*Strioterebrum*) Dall, 1908: 251. STEARNS, San Pedro, California [**1 paralectotype, USNM 32772 (not found)**]; Mrs. BURTON WILLIAMSON, San Pedro, California [**Lectotype, USNM 118806**, selected by Bratcher and Cernohorsky, as "holotype" (1987: 154, pl. 46, figs. 179a, b]. Oldroyd (1927: 60) cited both USNM lots as "Type" without further restriction. Terebridae.

periconis, Callistochiton Dall, 1908: 355–356. Perico Island, Panama Bay, on the reefs [**Holotype, USNM 110763** (see also Ferreira, 1979a: 458–460; Kaas and van Belle, 1994: 176–178)]. Ischnochitonidae.

perla, Poromya Dall, 1908: 428–429, plate 18, figures 2, 5. *Albatross* 3392 [**Holotype, USNM 122930** (figured by Bernard, 1974: 82–83, pl. 22, figs. 1, 2)]. Poromyidae.

pernodata, Gemmula esuriens Dall **var.** Dall 1908: 266. *Albatross* 3414 [**Holotype, USNM 123127** (see also Oldroyd, 1927: 77–78)]. Turridae.

peruviana, Clinura Dall, 1908: 293, plate 13, figure 2. *Albatross* 4654 [**Holotype, USNM 110564** (figured by McLean in Keen, 1971: fig. 1673)]. Turridae.

peruviana, Leda (*Leda*) "nom. prov." Dall, 1908: 377. *Albatross* 4654 [**Holotype (1v), USNM 110691**]. This name is a junior primary homonym of *Leda peruviana* Dall, 1898 (which was proposed as a replacement name for *Leda acuminata* Nelson, 1870, non Buch, 1845!). Nuculanidae.

peruviana, Malletia Dall, 1908: 384, plate 10, figures 3, 5. *Albatross* 4654 [**syntypes (1 specimen + 1v), USNM 110574** (as "holotype" in Scott et al., 1990: 9); **numerous syntypes (30 + v), USNM 110576**; **syntypes (6v), MCZ 27834**; **syntypes (1 specimen + 2v), SBMNH 34678**]. The "holotype" citation of Scott et al. (1990) is not a valid lectotype selection because a single specimen was not specified. Malletiidae.

peruvianum, Dentalium Dall, 1908: 358. *Albatross* 4656 ("the type specimen") [**Holotype, USNM 110667**]; *Albatross* 4649 [**1 paratype, USNM 110666** (fragment)]. Dentaliidae.

peruvianus, Cadulus (*Gadila*) Dall, 1908: 361. *Albatross* 4654 [**Lectotype, USNM 110671**; selected by Keen, as "holotype" (1971: 965, caption to figure 21); **2 paralectotypes, USNM 602250; 1 paralectotype, MCZ 27972**]; *Albatross* 2807 [**1 paralectotype, USNM 122806**]. Siphonodentaliidae.

pigafettae, Nucula Dall, 1908: 369–370. *Albatross* 2780 [**syntypes (1 specimen + 2v), USNM 96243**; **syntypes (4 specimens + 8v), USNM 604256**; **syntypes (1 specimen + 3v), MCZ 27807**]. Nuculidae.

pisum, Aligena Dall, 1908: 413. *Albatross* 2778 [**Holotype, USNM 110715**]. Transferred from Kelliidae to Thyasiridae by Harry (1969: 177–178, figs. 32, 33). Thyasiridae.

pizarro, Cylichnella (*Cylichnium*) Dall, 1908: 243, plate 11, figure 1. *Albatross* 3392 [**Holotype, USNM 123079**]. Cylichnidae.

planetica, Cuspidaria (*Cardiomya*) Dall, 1908: 433. *Albatross* 2925 ("types") [**Lectotype, USNM 110720**, selected by Oldroyd, as "Type" (1925: 99–100; see also Keen, 1971: 944, caption to fig. 783); **paralectotypes (5v), USNM 887579** (broken)]. Bernard (1974: 66) referred to USNM 110720 as "holotype" but then stated that "the type material consists of four syntypes," which is an inexplicable contradiction by Bernard. Dall also recorded this species from *Albatross* 3400, 3059, and 3609 and Captain's Harbor, Alaska, but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Cuspidariidae.

planeticus, Scaphander (*Sabatina*) Dall, 1908: 241. *Albatross* 3684 [**Holotype, USNM 110748**]. Cylichnidae.

plicatella, Clathurella Dall, 1908: 289. *Albatross* 2799 [**Holotype, USNM 110604** (figured by Dall, 1919: 7, pl. 20, fig. 4)]. Turridae.

polyleptus, Pecten (*Pseudamusium*) Dall, 1908: 403, plate 10, figure 9. *Albatross* 4642 [**Holotype (1v), USNM 110586** (figured by Grau, 1959: 43–44, pl. 16, fig. 1)]. Dall recorded a left valve from *Albatross* 2781, "which probably belongs to the same species . . . ," but this tentative statement did not specify that this latter lot represented type material. Pectinidae.

polystephanus, Pleurotomella (*Pleurotomella*) Dall, 1908: 281. *Albatross* 2808 [**Holotype, USNM 96498** (figured by McLean in Keen 1971: fig. 1652)]. Turridae.

pompholyx, Arca (*Bathyarca*) *corpulenta* Smith **var.?** Dall, 1908: 398. *Albatross* 4390 [**Lectotype, USNM 110704**, selected by Oldroyd, as "Type" (1925: 47)]; *Albatross* 4396 [**paralectotype (2v), USNM 602596**]; *Albatross* 4709 [**paralectotype (2v), USNM 110705** (broken)]; *Albatross* 4721 [**1 paralectotype (1v), USNM 110706** (broken)]; *Albatross* 4740 [**not found**]. Arcidae.

pseustes, Cuspidaria (*Cardiomya*) Dall, 1908: 431–433. *Albatross* 3392 [**Holotype, USNM 122939** (figured by Keen, 1971: fig. 784; Bernard, 1974: 68–69, pl. 18. figs. 3, 4)]. Cuspidariidae.

radialis, Architectonica Dall, 1908: 327–328. *Albatross* 3392 [**Holotype, USNM 123037** (figured by Keen, 1971: fig. 432; Bieler, 1993: 164–167, fig. 133)]. Architectonicidae.

resina, Turris (*Surcula*) Dall, 1908: 264. *Albatross* 3354 [**Holotype, USNM 123103** (figured by Dall, 1919: 16, pl. 2, fig. 4)]. Turridae.

rhytida, Leda (*Leda*) Dall, 1908: 376–377. *Albatross* 3422 [**Holotype, USNM 122918**]. Nuculanidae.

rochebrunei, Rochefortia Dall, 1908: 414, plate 17, figure 5. *Albatross* 2778 [**Holotype (1v), USNM 110713**]. Leptonidae.

rotunda, Oocorys Dall, 1908: 322, plate 4, figure 9. *Albatross* 3360 [**Holotype, USNM 123029**]. Cassidae.

rotundus, Pecten (*Cyclopecten*) Dall, 1908: 404–405. *Albatross* 2799 [**2 syntypes (3v), USNM 110708** (cited as "holotype" by Grau, 1959: 33)]; *Albatross* 2784 [**1 syntype (1v), USNM 122744**]. A junior homonym (non Hagenow, 1842); renamed *Pecten* (*Cyclopecten*) *pernomus* Hertlein, 1935 (pages 320–321). Propeamussiidae.

rubidus, Clanculus (*Panocochlea*) Dall, 1908: 346–347, plate 8, figures 3, 4. *Albatross* 3355 [**Lectotype, USNM 122953**, selected by McLean in Keen, as "holotype" (1971: 945, caption to fig. 143)]; *Albatross* 3396 [**1 paralectotype, USNM 122954**]. Turbinidae.

saccoi, Borsonia (*Borsonella*) Dall, 1908: 277. *Albatross* 3354 [**Holotype, USNM 123105** (figured by McLean in Keen, 1971: fig. 1761)]. Turridae.

salaria, Tindaria Dall, 1908: 387–388. *Albatross* 4693 [**syntypes (5v), USNM 110695** (broken)]. Nuculanidae.

scethra, Natica (*Cochlis*) Dall, 1908: 333,

plate 11, figure 5. *Albatross* 3391 [**Lectotype, USNM 123048**, selected by Marincovich, as "holotype" (1977: 382–383, pl. 37, fig. 7), **1 paralectotype, USNM 678716; 2 paralectotypes, MCZ 27953**]. Naticidae.

sedillina, Mangilia Dall, 1908: 287, plate 13, figure 8. *Albatross* 3392 [**Lectotype, USNM 123116**, selected by McLean in Keen, as "holotype" (1971: 961, caption to fig. 1854); **1 paralectotype, USNM 887594; 1 paralectotype, MCZ 27909**]. Turridae.

serilla, Gemmula Dall, 1908: 269, plate 13, figure 6. *Albatross* 3392 [**Lectotype, USNM 123123**, selected by McLean in Keen, as "holotype" (1971: 958, caption to fig. 1674); **1 paralectotype, MCZ 27898**]. Turridae.

similaris, Lima (*Limatula*) Dall, 1908: 408. *Albatross* 2799 [**syntype, USNM 109034** (lost); **syntype, USNM 129319** (also lost!)]. Dall noted that "[o]nly one valve of this little shell was obtained, and that was unfortunately crushed by accident after the above diagnosis had been prepared. A second specimen, somewhat smaller, was obtained at [*Albatross*] 2983 . . ."; however, this latter specimen is lost (there is an empty vial in the tray for that lot). Keen (1971: 938, caption to fig. 218) stated that USNM 109034 was the "holotype" figured in her book; this is certainly incorrect, as that lot was crushed. Presumably it was USNM 129319 that was actually illustrated by Keen. Limidae.

smirna, Tindaria Dall, 1908: 389, plate 17, figures 6, 7. *Albatross* 3360 [**Holotype, USNM 122919**]. Nuculanidae.

smithii, Cetoconcha Dall, 1908: 431, plate 18, figure 10. *Albatross* 3415 [**Holotype, USNM 122943** (broken) (figured by Bernard, 1974: 85–86, pl. 26, fig. 5)]. Poromyidae.

stephanica, Seguenzia Dall, 1908: 325–326. *Albatross* 3431 [**Lectotype, USNM 123034**, selected by McLean in Keen, as "holotype" (1971: 945, caption to fig. 178); **1 paralectotype, MCZ 27932**]. Seguenziidae.

stimpsoni, Limopsis Dall, 1908: 396. *Albatross* 3392 [**Lectotype, USNM 122881**, selected by Keen, as "holotype" (1971: 936, caption to fig. 108)]; *Albatross* 3393 [**1 paralectotype, USNM 122882**]. Limopsidae.

strebeli, Polinices (*Euspira*) Dall, 1908: 338. *Albatross* 2783 ("type") [**Holotype, USNM 97093**]. Dall also recorded this species from *Albatross* 2777 and 2808, but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Naticidae.

stylus, Terebra (*Perirhoe*?) Dall, 1908: 253. STEARNS, Panama Bay [**Holotype, USNM 32773** (figured by Keen, 1958: fig. 954; 1971: fig. 1546)]. Bratcher and Cernohorsky (1987: 52, 54, pl. 8, fig. 25b) questioned the type locality and synonymized this taxon with the Indo-Pacific *Terebra laevigata* Gray, 1834. Terebridae.

subequalis, Sphenia Dall, 1908: 422–423. *Albatross* 2779 [**Holotype (1v), USNM 110719**]. Myidae.

suteri, Limia [sic = *Lima*] (*Limatula*) Dall, 1908: 410. H. SUTER, Stewart Island, New Zealand, 18 fm [**1 syntype (1v), USNM 195290**; **syntypes (3v), USNM 679270**]. Limidae.

taeniolata, Nucula Dall, 1908: 368–369, plate 7, figures 3, 5. *Albatross* 3417 [**syntypes (6v), USNM 122897**; **syntypes (1 specimen + 2v), USNM 153319**; **syntypes (1 specimen + 1v), MCZ 27805**]. Nuculidae.

tanneri, Nucula Dall, 1908: 367. *Albatross* 2780 [**1 syntype, USNM 96243; 1 syntype, USNM 604255**; **syntypes (4v), MCZ 27813**]; *Albatross* 2781 [**syntypes (6v), USNM 96222**]; *Albatross* 2783 [**syntypes (1 specimen + 2v), USNM 96909**]; *Albatross* 2784 [**syntypes (1 specimen + 2v), USNM 122737**]; *Albatross* 2787 [**syntypes (2 specimens + 2v), USNM 96938**]. Nuculidae.

thalassoma, Glyphostoma Dall, 1908: 290. *Albatross* 3017 [**Holotype, USNM**

110612 (figured by by McLean in Keen, 1971: fig. 1784)]. Turridae.

thea, Tindaria Dall, 1908: 390. *Albatross* 4654 [**1 syntype, USNM 110577** (broken); **1 syntype, MCZ 27830**]. Nuculanidae.

truncata, Malletia Dall, 1908: 384–385, plate 17, figure 1. *Albatross* 3374 [**1 syntype, USNM 122906**]; *Albatross* 3361 [**1 syntype, USNM 122905**]; *Albatross* 3381 [**syntype (2v), USNM 122907** (broken)]. Malletiidae.

turbinum, Epitonium (*Sthenorhytis*) Dall, 1908: 317, plate 9, figures 5, 6, 8. *Albatross* 4642 [**Holotype, USNM 110568** (broken) (figured by Keen, 1971: fig. 665)]. Epitoniidae.

vaginatus, Polinices (*Euspira*) Dall, 1908: 336–337. *Albatross* 2778 [**6 syntypes, USNM 96231; 1 syntype, USNM 106873**]; *Albatross* 2779 [**1 syntype, USNM 97126; 2 syntypes, USNM 678711; 1 syntype, MCZ 27947**]; at Laredo Bay in the [Magellan] strait [**1 syntype, USNM 110658**]. Naticidae.

vexillata, Tritonoharpa Dall, 1908: 320, plate 8, figure 7. *Albatross* 4642 [**Holotype, USNM 110580** (figured by Keen, 1971: fig. 973)]. Transferred from Buccinidae to Cancellariidae by Beu and Maxwell (1987: 47, pl. 25, figs. a–g, j). Cancellariidae.

vicella, Gemmula Dall, 1908: 268–269, plate 14, figure 5. *Albatross* 3392 [**Holotype, USNM 123122** (figured by McLean in Keen, 1971: fig. 1867)]. Turridae.

vincula, Yoldia (*Katadesmia*) Dall, 1908: 379, plate 5, figure 5. *Albatross* 3360 [**syntypes (1 specimen + 2v), USNM 122903**; **1 syntype (2v), MCZ 27835** (broken)]; *Albatross* 3354 [**1 syntype (2v), USNM 122902**]; *Albatross* 3361 [**1 syntype (1v), USNM 122904**]. Nuculanidae.

xylona, Pleurotomella (*Gymnobela*) Dall, 1908: 280, plate 2, figure 3. *Albatross* 3413 [**Holotype, USNM 123111** (figured by McLean in Keen, 1971: fig. 1868)]. Turridae.

zonalis, Limopsis Dall, 1908: 393–394, plate 7, figures 6, 9. *Albatross* 3356 ("type") [**Holotype, USNM 122878**; **numerous paratypes (9 specimens + 4v), USNM 887595; 2 paratypes, SBMNH 34679** (ex USNM 122878)]. Dall also recorded this species from *Albatross* 3357, 3358, and 4630, but such records are excluded from the type series [ICZN Article 72(b)(vi)]. Limopsidae.

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GENERIC INDEX

Bivalvia

Aligena
borniana
pisum
Amusium (*Propeamusium*)
malpelonium
Arca (*Bathyarca*)
nucleator
pompholyx
Arca (*Cucullaria*)
endemica
Cetoconcha
smithii
Corbula (*Cuneocorbula*)
ira
Corneocyclas
magellanicus
Cuspidaria
panamensis
Cuspidaria (*Cardiomya*)
planetica
pseustes
Leda (*Jupiteria*)
acrita
agapea
callimene
lobula
Leda (*Leda*)
cordyla
loshka
peruviana
rhytida
Leda (*Spinula*)
calcar
calcarella
Lima (*Acesta*)
diomedae
Lima (*Limatula*)
similaris
suteri
Limopsis
diazi
diegensis
juarezi
mabilliana
stimpsoni
zonalis
Lyonsia
panamensis
Lyonsiella
pacifica
Macoma
hupeana
Macoma (*Psammacoma*)
hesperus
Malletia
inequalis
peruviana
truncata
Malletia (*Minormalletia*)
arciformis
benthima
Myonera
garretti
Nucula
agujana
chrysocoma
colombiana
panamina
pigafettae
taeniolata
tanneri
Pecten (*Chlamys*)
pasca
Pecten (*Cyclopecten*)
cocosensis
rotundus
Pecten (*Pallium*)
miser
Pecten (*Pseudamusium*)
liriope
neoceanicus
panamensis
polyleptus
Phaseolus (*Silicula*)
patagonicus
Pholadidea (*Penitella*)
minuscula
Poromya
perla
Poromya (*Dermatomya*)
chilensis
equatorialis
Protocardia
panamensis
Rochefortia
mabillei
rochebrunei
Solemya (*Acharax*)
agassizii
Solemya (*Petrasma*)
panamensis
Sphenia
subequalis
Tellina (*Moerella*)
chrysogona
Tellina (*Phyllodina*)
fluctigera
Tindaria
atossa
compressa
mexicana
panamensis
salaria
smirna
thea
Vesicomya
donacia

Xylophaga
mexicana
Yoldia (*Katadesmia*)
vincula
Yoldia (*Orthoyoldia*)
panamensis
Yoldia (*Yoldiella*)
chilenica
dicella
granula
indolens
infrequens
leonilda
mantana

Gastropoda

Acteon
panamensis
Acteon (*Microglyphis*)
estuarinus
mazatlanicus
Alectrion (*Hima*)
catallus
miser
Alectrion (*Tritia*)
exsarcus
goniopleura
Architectonica
radialis
Bathysciadium
pacificum
Borsonia (*Borsonella*)
agassizii
coronadoi
diegensis
saccoi
Bullaria (*Leucophysema*)
morgana
Bursa (*Lampadopsis*)
calcipicta
Cancellaria (*Admete*)
californica
Cancellaria (*Merica*)
corbicula
microsoma
Cancellaria (*Narona*)
exopleura
Capulus
chilensis
Cavolina
occidentalis
Cerithioderma
pacifica
Clanculus (*Panocochlea*)
rubidus
Clathurella
orariana
panamella
plicatella
Clinura
monochorda
peruviana
Cocculina
agassizii
diomedae
nassa
Columbella (*Anachis*)
fusidens
Cylichnella (*Bullinella*)
inca
Cylichnella (*Cylichnium*)
atahualpa
pizarro
Daphnella (*Eubela*)
imparella
Daphnella (*Surculina*)
blanda
cortezi
Drillia
decenna
Epitonium (*Ferminoscala*)
brunneopictum
ferminianum
Epitonium (*Sthenorhytis*)
turbinum
Fusinus
fragillissimus
panamensis
Gemmula
benthima
eldorana
esuriens
herilda
pernodata
serilla
vicella
Glyphostoma
immaculata
thalassoma
Hipponix
delicata
Irenosyrinx
crebristriata
leonis
Leptothyra
panamensis
Leucosyrinx
clionella
erosina
pacifica
Liotia (*Arene*)
californica
pacis
Mangilia
cetolaca
encella
enora
genilda
movilla
sedillina

Murex (*Tritonalia*)
diomedaeus
Natica (*Cochlis*)
othello
scethra
Oocorys
elevata
rotunda
Petaloconchus
complicatus
Pleurotomella (*Gymnobela*)
altina
egregia
isogonia
xylona
Pleurotomella (*Phymorhynchus*)
clarinda
oceanica
Pleurotomella (*Pleurotomella*)
dinora
esilda
parella
polystephanus
Polinices (*Euspira*)
agujanus
constrictus
crawfordianus
litorinus
pardoanus
strebeli
vaginatus
Ptychatractus
californicus
Scaphander
cylindrellus
decapitatus
Scaphander (*Sabatina*)
planeticus
Seguenzia
occidentalis
stephanica
Solariella
equatorialis
galapagana
Solenosteira
elegans
Stilifer (*Mucronalia*)
bathymetrae
Strombina
edentula
Terebra (*Perirhoe*)
stylus
Terebra (*Strioterebrum*)
balaenorum
bridgesi
lucana
panamensis
pedroana
Thais
nesiotes
Tritonoharpa
vexillata
Trophon (*Pascula*)
citricus
Troschelia (*Thalassoplanes*)
mörchii
Turris (*Surcula*)
armilda
dolenta
dotella
fusinella
notilla
resina
Turritella
mariana
Volutopsius
amabilis

Polyplacophora

Callistochiton
periconis
Ischnochiton
ophioderma
Lepidopleurus
abbreviatus
incongruus
opacus

Scaphopoda

Cadulus (*Gadila*)
peruvianus
Dentalium
panamense
peruvianum

APPENDIX: DATA FOR *ALBATROSS* STATIONS THAT REPRESENT TYPE LOCALITIES OF DALL (1908) SPECIES

Dall (1908: 446–476) provided data for stations 3353–3437 and 4567–4743; for the remaining stations, see *Albatross* (1903, 1906), Fassett (1904), and Townsend (1901). For all stations, I have added a generalized geographical description for the reader's convenience. For five stations (4339, 4353, 4382, 4407, and 4425), Townsend gave "bearings" (instead of latitude and longitude), which I converted into approximate geographical indications. My editorial additions should not be used for navigational purposes.

Station	Fathoms	Locality	Date
2772	31.5	52°16′00″S, 68°13′00″W Off Cabo Virgins, east entrance of Magellan Strait	January 17, 1888
2777	19.75	52°38′00″S, 70°10′30″W Magellan Strait, Chile	January 19, 1888
2778	61	53°1′00″S, 70°42′15″W Magellan Strait, Chile	January 23, 1888
2779	77.5	53°6′00″S, 70°40′30″W Magellan Strait, Chile	January 23, 1888
2780	369	53°1′00″S, 73°42′30″W Archipiélago de la Reina Adelaida, Chile	February 2, 1888
2781	348	51°52′00″S, 73°41′00″W Off W coast of Patagonia, Chile	February 4, 1888
2782	258	51°12′00″S, 74°13′30″W Off W coast of Patagonia, Chile	February 6, 1888
2783	122	51°2′30″S, 74°8′30″W Off W Coast of Patagonia, Chile	February 6, 1888
2784	194	48°41′00″S, 74°24′00″W Canal Messer, southern Chile	February 8, 1888
2785	449	48°9′00″S, 74°36′00″W Canal Messer, southern Chile	February 8, 1888
2787	61	46°47′30″S, 75°15′00″W Off Peninsula de Talteco, Chile	February 9, 1888
2792	401	0°37′00″S, 81°00′00″W Off Manta, Ecuador	March 2, 1888
2793	741	1°3′00″N, 80°15′00″W Off Punta Galera, Ecuador	March 3, 1888
2794	62	7°37′00″N, 78°46′30″W Golfo de Panama	March 5, 1888
2798	18	8°10′30″N, 78°50′30″W Golfo de Panama	March 5, 1888
2799	29.5	8°44′00″N, 79°9′00″W Golfo de Panama	March 6, 1888
2800	7	8°51′00″N, 79°31′30″W Golfo de Panama	March 30, 1888
2801	14	8°47′00″N, 79°29′30″W Golfo de Panama	March 30, 1888
2803	26	8°27′00″N, 79°35′00″W Golfo de Panama	March 30, 1888
2804	47	8°16′30″N, 79°37′45″W Golfo de Panama	March 30, 1888
2805	51.5	7°56′00″N, 79°41′30″W Golfo de Panama	March 30, 1888
2807	812	0°24′00″S, 89°06′00″W E of Isla San Cristóbal, Galápagos	April 4, 1888

Station	Fathoms	Locality	Date
2808	634	0°36′30″S, 89°19′00″W E of Isla San Cristóbal, Galápagos	April 4, 1888
2823	26.5	24°18′00″N, 110°22′00″W Bahia de La Paz, Baja California, Mexico (Gulf of California)	April 30, 1888
2830	66	23°33′00″N, 110°37′00″W W of Todos Santos, Baja California, Mexico	May 1, 1888
2834	48	26°14′00″N, 113°13′00″W SE of Punta Abreojos, Baja California, Mexico	May 3, 1888
2835	5.5	26°42′30″N, 113°34′15″W SE of Punta Abreojos, Baja California, Mexico	May 4, 1888
2839	414	33°8′00″N, 118°40′00″W NW of San Clemente Island, California, USA	May 8, 1888
2859	1,569	55°20′00″N, 136°20′00″W SW of Sitka, Alaska, USA	August 29, 1888
2919	984	32°17′00″N, 119°17′00″W SW of San Clemente Island, California, USA	January 17, 1889
2923	822	32°40′30″N, 117°31′30″W W of San Diego, California, USA	January 19, 1889
2925	339	32°32′30″N, 117°24′00″W W of San Diego, California, USA	January 19, 1889
2931	34	32°25′30″N, 117°16′45″W Off Los Coronados Islands, NW of Rosarito, Baja California, Mexico	January 26, 1889
2936	359	32°49′00″N, 117°27′30″W W of San Diego, California, USA	February 4, 1889
2973	68	34°19′30″N, 119°44′15″W SW of Santa Barbara, California, USA	February 11, 1889
2980	603	33°49′45″N, 119°24′30″W S of Anacapa Island, California, USA	February 12, 1889
2984	113	28°57′15″N, 118°15′45″W Off Guadalupe Island, Mexico	February 28, 1889
2996	112	24°30′15″N, 110°29′00″W Bahia de la Paz, Baja California, Mexico (Gulf of California)	March 16, 1889
3017	58	29°54′30″N, 113°01′00″W W of Cabo Lobos, Sonora, Mexico (Gulf of California)	March 24, 1889
3034	24	30°36′30″N, 114°27′45″W S of Punta Estrella, Baja California, Mexico (Gulf of California)	March 27, 1889
3074	887	47°22′00″N, 125°48′30″W W of Taholah, Olympic Peninsula, Washington, USA	June 29, 1889
3194	92	35°23′30″N, 121°2′30″W W of Morro Bay, California, USA	April 5, 1890

Station	Fathoms	Locality	Date
3346	786	45°30′00″N, 124°52′00″W W of Cape Meares, Oregon, USA	September 22, 1890
3354	322	7°9′45″N, 80°50′00″W S of Cabo Cambutal, Panama	February 23, 1891
3355	182	7°12′20″N, 80°55′00″W S of Cabo Cambutal, Panama	February 23, 1891
3356	546	7°9′30″N, 81°8′30″W SW of Cabo Cambutal, Panama	February 23, 1891
3357	782	6°35′00″N, 81°44′00″W S of Isla Jicarón, Panama	February 24, 1891
3358	555	6°30′00″N, 81°44′00″W S of Isla Jicarón, Panama	February 24, 1891
3360	1,672	6°17′00″N, 82°5′00″W SW of Isla Jicarón, Panama	February 24, 1891
3361	1,471	6°10′00″N, 83°6′00″W S of Punta Burica, Panama	February 25, 1891
3365	1,010	5°31′00″N, 86°31′00″W SW of Cabo Blanco, Costa Rica	February 27, 1891
3366	1,067	5°30′00″N, 86°45′00″W SW of Cabo Blanco, Costa Rica	February 27, 1891
3368	66	5°32′45″N, 86°54′30″W SW of Cabo Blanco, Costa Rica	February 28, 1891
3369	52	5°32′45″N, 86°55′20″W SW of Cabo Blanco, Costa Rica	February 28, 1891
3374	1,823	2°35′00″N, 83°53′00″W SW of Isla De Malpelo, Colombia	March 3, 1891
3376	1,132	3°9′00″N, 82°8′00″W SW of Isla de Malpelo, Colombia	March 4, 1891
3380	899	4°3′00″N, 81°31′00″W Off Isla de Malpelo, Colombia	March 5, 1891
3381	1,772	4°56′00″N, 80°52′30″W NE of Isla de Malpelo, Colombia	March 6, 1891
3382	1,793	6°21′00″N, 80°41′00″W Golfo de Panama	March 7, 1891
3387	127	7°40′00″N, 79°17′50″W Golfo de Panama	March 8, 1891
3389	210	7°16′45″N, 79°56′30″W Golfo de Panama	March 9, 1891
3391	153	7°33′40″N, 79°43′20″W Golfo de Panama	March 9, 1891
3392	1,270	7°5′30″N, 79°40′00″W Golfo de Panama	March 10, 1891

Station	Fathoms	Locality	Date
3393	1,020	7°15′00″N, 79°36′00″W Golfo de Panama	March 10, 1891
3394	511	7°21′00″N, 79°35′00″W Golfo de Panama	March 10, 1891
3395	730	7°30′36″N, 78°39′00″W Golfo de Panama	March 11, 1891
3396	259	7°32′00″N, 78°36′30″W Golfo de Panama	March 11, 1891
3397	85	7°33′00″N, 78°34′20″W Golfo de Panama	March 11, 1891
3398	1,573	1°7′00″N, 80°21′00″W NW of Punta Galera, Ecuador	March 23, 1891
3399	1,740	1°7′00″N, 81°4′00″W NW of Punta Galera, Ecuador	March 24, 1891
3404	385	1°3′00″S, 89°28′00″W S of Can Cristóbal, Galápagos	March 28, 1891
3407	885	0°4′00″S, 90°24′30″W N of Isla San Salvador, Galápagos	April 3, 1891
3413	1,360	2°34′00″N, 92°6′00″W NW of Isla Culpepper, Galápagos	April 5, 1891
3414	2,232	10°14′00″N, 96°28′00″W East Guatemala Basin (SW of Tehuantepec, Mexico)	April 8, 1891
3415	1,879	14°46′00″N, 98°40′00″W SE of Acapulco, Guerrero, Mexico	April 10, 1891
3417	493	16°32′00″N, 99°48′00″W SE of Acapulco, Guerrero, Mexico	April 11, 1891
3418	660	16°33′00″N, 99°52′30″W S of Acapulco, Guerrero, Mexico	April 11, 1891
3422	141	16°47′30″N, 99°59′30″W S of Acapulco, Guerrero, Mexico	April 12, 1891
3427	80	21°22′15″N, 106°25′00″W S of Islas Marias, Nayarit, Mexico	April 18, 1891
3431	995	23°59′00″N, 108°40′00″W NE of Punta Arena, Baja California, Mexico (Gulf of California)	April 20, 1891
3434	1,588	25°29′30″N, 109°48′00″W E of Isla Santa Cruz, Baja California, Mexico (Gulf of California)	April 21, 1891
3681	2,368	28°23′00″N, 126°57′00″W W of Isla Guadalupe, Mexico	August 27, 1891
3683	2,690	9°57′00″N, 137°47′00″W Clipperton Fracture Zone, mid-Pacific	September 5, 1891
3684	2,463	0°50′00″N, 137°54′00″W S of Clipperton Fracture Zone, mid-Pacific	September 10, 1891

Station	Fathoms	Locality	Date
4339	287–369	SW of Point Loma, San Diego, California, USA	March 10, 1904
4353	628–640	SW of Point Loma, San Diego, California, USA	March 14, 1904
4382	642–666	SW of North Island, Coronado, San Diego, California, USA	March 18, 1904
4390	1,350–2,182	33°2′15″N, 120°42′00″W W of San Nicolas Island, California, USA	March 28, 1904
4396	2,228	33°1′35″N, 121°32′—″W W of San Nicolas Island, California, USA	March 31, 1904
4407	478–600	SE of Santa Catalina Island, California, USA	April 9, 1904
4425	1,084–1,100	NE of San Nicolas Island, California, USA	April 13, 1904
4630	556	6°53′—″N, 81°42′30″W S of Isla Jicarón, Panama	November 3, 1904
4641	633	1°34′24″S, 89°30′12″W SE of Isla Espanola, Galápagos	November 7, 1904
4642	300	1°30′30″S, 89°35′—″W SE of Isla Espanola, Calápagos	November 7, 1904
4643	100	1°28′42″S, 89°48′30″W S of Isla Espanola, Galápagos	November 7, 1904
4647	2,005	4°33′—″S, 87°42′30″W SE of Galápagos	November 9, 1904
4649	2,235	5°17′–″S, 85°19′30″W SE of Galápagos	November 10, 1904
4654	1,036	5°46′—″S, 81°31′54″W W of Punta Aguja, Peru	November 12, 1904
4656	2,222	6°54′36″S, 83°34′18″W SW of Chiclayo, Peru	November 13, 1904
4658	2,370	8°29′30″S, 85°35′36″W W of Trujillo, Peru	November 14, 1904
4672	2,845	13°11′36″S, 78°18′18″W SW of Lima, Peru	November 21, 1904
4685	2,205	21°36′12″S, 94°56′—″W Peru Basin	December 10, 1904
4693	1,142	26°30′6″S, 105°45′12″W SW of Isla Sala y Gómez	December 14, 1904
4709	2,035	10°15′12″S, 95°40′48″W Peru Basin	December 30, 1904
4721	2,084	8°7′30″S, 104°10′30″W E of East Pacific Ridge	January 15, 1905
4732	2,012	16°32′30″W, 119°59′—″W W of East Pacific Ridge	January 21, 1905
4740	2,422	9°2′6″S, 123°20′6″W W of East Pacific Ridge	February 11, 1905

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JOHN E. CADLE

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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JOHN E. CADLE[1]

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ABSTRACT. Two new species of the colubrid snake genus *Geodipsas* are described from eastern Madagascar. *Geodipsas laphystia*, new species, has been confused with the widespread *G. infralineata* and is apparently sympatric with *infralineata* over a broad area of eastern Madagascar. The two are distinguished by subtle aspects of dorsal pattern (fine longitudinal lines in *laphystia* vs. indistinct chevrons or diagonals in *infralineata*), by hemipenial morphology, and by differences in maximal body size. *Geodipsas zeny*, new species, is described on the basis of three specimens from rainforests between approximately 19° and 23°35' south latitude. It is smaller than other species of Malagasy *Geodipsas* and has low numbers of ventrals and subcaudals, paired dark nape blotches or a collar, a bold midventral dark line, and a brown dorsum with a dark network of lines that tends to form longitudinal streaks posteriorly.

Comparison of types and other specimens referred to *Geodipsas heimi* Angel (1936) and *Tachymenis* [now *Geodipsas*] *boulengeri* Peracca (1892) reveals that these are the same taxon and the two are synonymized. Six species of Malagasy *Geodipsas* are recognized (*boulengeri, infralineata, laphystia, vinckei, zeny*, and a species discussed herein as *Geodipsas* species inquirenda); a key for their identification is provided. Taxonomic and natural history data are summarized for *G. boulengeri* and *G. infralineata* in addition to the newly described species. *Geodipsas infralineata* and *G. laphystia* are nocturnal arboreal predators on frogs, and in *laphystia* a high proportion of dietary items were also aerial egg clutches of *Mantidactylus* spp. (Anura: Ranidae); larger individuals of *infralineata* also consume mammals. Natural history data for other species of Malagasy *Geodipsas* are scant.

Geodipsas is currently the only colubrid genus

[1] Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

shared between Madagascar and Africa. To help clarify the relationships of the species, hemipenes of four species of Malagasy *Geodipsas* (*boulengeri, infralineata, laphystia, zeny*) and the three African species (*depressiceps, procterae, vauerocegae*) are described. Hemipenes of the four Malagasy species are similar in structure and ornamentation, including the derived characters of nonbilobation and distal division of the sulcus spermaticus. The sulcus spermaticus is centrolineal in orientation and the organs are entirely spinose. Although hemipenes of the African species of *Geodipsas* are nonbilobed and have a centrolineal sulcus, their hemipenes are otherwise dissimilar to the Malagasy species. Moreover, whereas hemipenes of the east African species, *G. procterae* and *G. vauerocegae*, share unusual apical structures and are otherwise extremely similar, the hemipenis of the central African *G. depressiceps* has unusual longitudinal ridges and bears little resemblance to that of the other African species. Incidental observations on the skull morphology and pupil form of *Geodipsas* are presented. The pupil is broadly elliptical (subcircular), as contrasted with a round or narrowly elliptical (slitlike) form, as has been reported in the literature.

Examination of the basis for including African species in *Geodipsas* (type species: *Geodipsas infralineata*) shows that conclusion to be based on little evidence of relationship. Thus, the monophyly of *Geodipsas* is questioned. Other than the derived character of loss of hemipenial bilobation, which has evolved many times within colubrids, few special similarities exist in known morphological characters of the African and Malagasy species. A nonbilobed hemipenis is present in at least one other Malagasy genus, *Alluaudina,* thus calling into question its relevance in defining a monophyletic *Geodipsas sensu lato. Alluaudina* also shares with Malagasy *Geodipsas* a broadly elliptical pupil, an unusual condition. These shared characters suggest that *Alluaudina* may be among the closest relatives of Malagasy species of *Geodipsas.* The conclusion that the three African species are monophyletic *inter se* is also questioned because of the morphological disparity between *G. depressiceps* and the other two species. On the other hand, Malagasy *Geodipsas* share basic and detailed similarities in hemipenial morphology that suggest their close relationship.

Among the Malagasy species of *Geodipsas, laphystia* and *infralineata* share putative derived characters associated with arboreality; *boulengeri* and a species of *Geodipsas* previously confused with *"heimi"* from the vicinity of Montagne d'Ambre share putative derived similarities of color pattern and sulcus spermaticus. The species of each of these pairs are presumed sister taxa. *Geodipsas zeny* and *G. vinckei* are of uncertain relationship to the other species.

INTRODUCTION

Geodipsas Boulenger is currently the only genus of colubrid snakes, and one of few reptile genera, shared by Madagascar and the African mainland. Rasmussen et al. (1995) reviewed two of the three African species. Four Malagasy species are recognized in recent literature (Guibé, 1958; Brygoo, 1983; Glaw and Vences, 1994): *infralineata* (Günther, 1882), *boulengeri* (Peracca, 1892), *heimi* Angel (1936), and *vinckei* Domergue (1988). A survey of the herpetofauna of the Ranomafana National Park (referred to in the text simply as "Ranomafana" or **RNP**) in eastern Madagascar has revealed several new species of amphibians and reptiles and required partial revision or clarification of the status of some others (Cadle, 1995, 1996). During the RNP survey, four species of *Geodipsas* were collected, and this paper summarizes their taxonomy and natural history. One of the RNP snakes, *Geodipsas infralineata,* is the best known of all the Malagasy species of *Geodipsas,* although, as indicated later, an undescribed species has heretofore been confused with it. That undescribed species and another one are described as new herein. Determining the identity of the fourth RNP species required consideration of the status of *Tachymenis boulengeri* Peracca (1892) and *Geodipsas heimi* Angel (1936). Evidence is presented indicating that these names refer to the same taxon. As the oldest available name is *Tachymenis boulengeri* Peracca, *Geodipsas heimi* Angel is synonymized with it.

MATERIALS AND METHODS

My study of *Geodipsas* is based primarily on specimens collected during the RNP survey, but I have incorporated data from other specimens (see *Specimens Examined*) in connection with museum surveys. Most natural history observations are from the RNP, although for the widespread species *G. infralineata* I have included personal and published observations from other localities.

Hemipenial terminology follows Myers (1973, 1974) and Myers and Campbell (1981), and procedures for their descrip-

tion and illustration are described by Cadle (1996). All everted organs were inflated with colored jelly to enhance the surface ornamentation prior to description. For visualization of mineralized hemipenial spines in one instance (*Remarks* in the account for *Geodipsas laphystia,* new species), I hydrated the organs, placed them in 2% potassium hydroxide (KOH) containing several drops of saturated alizarin red S overnight, destained them in 2% KOH, and processed them through a graded series of glycerin/ethanol mixtures, finally storing them in 70% ethanol.

Head proportions were measured with dial calipers to the nearest 0.01 mm; other measurements were made to the nearest millimeter with a ruler. For descriptions of vertebral hypapophyses, I followed the terminology and general descriptive protocols of Malnate (1972).

Coordinates for localities were derived from maps (1:50,000, 1:100,000, or 1:1,000,000) published by the Foiben-Taosarintanin'i Madagasikara, Antananarivo (FTM), or from the Defense Mapping Agency (1989) gazetteer. Specific localities within the RNP (see *Specimens Examined*) are mapped in Cadle (1995).

Recorded dietary items are derived from field observations of feeding, palping freshly collected specimens, or (rarely) dissections. However, I have not routinely surveyed museum specimens for food items, so observations reflect primarily diets within the RNP and other areas of southeastern Madagascar I have investigated.

DESCRIPTIONS OF NEW SPECIES

The first species described has been confused with *Geodipsas infralineata* for at least much of this century, including recent literature (e.g., Glaw and Vences, 1994). During study of specimens of "*infralineata*" from the RNP, it became clear that two species, distinguishable by hemipenial, scale, and pattern characteristics, were present. The new species appears to be sympatric with *infralineata* over a broad area of eastern Madagascar but, because earlier literature records for "*infralineata*" may refer to the new species, the details of distributions of these two similar species remain to be worked out. This new species is to be known as follows.

Geodipsas laphystia, new species
Figures 1, 3; Table 1

Geodipsas infralineata (not of Günther), part. *Geodipsas laphystia* has been confused with *G. infralineata* previously, including some or all of the following recent literature. Earlier references to *infralineata* will need to be verified with reference to voucher specimens to see whether *laphystia* is represented: Guibé, 1958:235; Brygoo, 1983:42, 55, 1987:23; Nicoll and Langrand, 1989:135; UICN, PNUE, and WWF, 1990:222; Glaw and Vences, 1992:264, 1994:346; Raxworthy and Nussbaum, 1994:68. Published figures of "*G. infralineata*" in Glaw and Vences (1992:figs. 326–327, 1994:figs. 514–515) are actually illustrations of *G. laphystia,* as shown by the diagnostic longitudinal lines (see *Diagnosis*).

Holotype. **Museum of Comparative Zoology, Harvard (MCZ) 181390** (field number JEC 13169), an adult male in good condition (Fig. 1). Specimen obtained 2 January 1996 by John E. Cadle.

Type Locality (Fig. 2). Talatakely, Ranomafana National Park, 950–1,000 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°16′S, 47°25′E].

Paratypes. The following specimens from the same locality as the holotype (elevations vary slightly, 950–1100 m): **MCZ 180339** (JEC 11814), adult female, 6 December 1992; **MCZ 180340–41** (JEC 12341–42), adult females, 1 January 1993; **MCZ 180342** (JEC 12365), adult male, 2 January 1993; **MCZ 181148** (JEC 9640), subadult male, 25 October 1990; **MCZ 181150–51** (JEC 10110–11), adult females, and **MCZ 181152** (JEC 10112), (adult ?) male, 4 December 1990; **MCZ 181164** (JEC 11815), adult female (skin + complete skeleton), 6 December 1992; **MCZ 181165** (JEC 12366), adult female (skin + complete skeleton), 2 January 1993; **MCZ 181391–92** (JEC 13064–65),

adult males, 30–31 December 1995; **MCZ 181393–94** (JEC 13077–78), adult female and male, 30–31 December 1995; **MCZ 181387–89** (JEC 13166–68), adult males, 2 January 1996.

MCZ 180343 (JEC 12279), adult female, 30 December 1992: Vatoharanana, Ranomafana National Park, 1,000 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°17′20″S, 47°25′45″E]. **MCZ 181158–59** (JEC 12629–30), adult females, 12 January 1993: Approximately 7 km SW (airline) Midongy du Sud [Midongy Atsimo], near Rianambo ("high waterfall") on Lalampo River,[2] 670 m, Fivondronana Midongy du Sud, Fianarantsoa Province, Madagascar [23°39′S, 46°57′E]. **MCZ 181395** (JEC 13267), subadult female, 8–11 January 1996: Vevembe Forest,[3] 22 km W (by road to Maropaika) Vondrozo, 550 m, Fivondronana Vondrozo, Fianarantsoa Province, Madagascar [22°47′S, 47°12′E].

Distribution (Fig. 2). From at least the vicinity of Midongy Atsimo (= Midongy du Sud; 23°39′S, 46°57′E) in the southeast to central Madagascar in the vicinity of Andasibe (18°56′S, 48°25′E; photos of *laphystia* identified as *infralineata* in Glaw and Vences, 1994:figs. 514–515). The northern distributional limits are unclear because *G. laphystia* has been confused with the widespread species *G. infralineata,* which has been reported from as far north as Montagne d'Ambre (12°30′S, 49°10′E; Glaw and Vences, 1994:344 [map]; Raxworthy and Nussbaum, 1994). The known elevational distribution of *G. laphystia* is approximately 550–1,100 m, the range encompassed by the type series.

The known geographic ranges of *Geodipsas laphystia* and *G. infralineata* are nearly coextensive, but I have not attempted to extensively document the the northern limits of either species (Figs. 2, 9). The two species are known to be sympatric in the vicinity of Midongy du Sud, in the RNP, and in the Perinet reserve (= Andasibe) (the preceding specimens and those in *Specimens Examined*). In the RNP, the two species may be segregated by habitat (see *Natural History*).

Etymology. Laphystia is a Greek adjective meaning "gluttonous." It refers to the seemingly voracious appetite these little snakes have for egg clutches of frogs of the genus *Mantidactylus* (see Natural History).

Diagnosis. A species of *Geodipsas* characterized by a relatively high number of ventrals (170–187) and subcaudals (64–81); posterior dorsal scale reduction usually by loss of row 4 or fusion of 4 + 5; compressed body and relatively long tail (21–26% of total length); and, in life, a yellow, gray, or brown ground color, upon which is superimposed a series of fine dark longitudinal lines usually evident on the suture line between dorsal scale rows 4–5 anteriorly (3–4 posteriorly), the suture line between rows 7–8, on the border between the ventrals and dorsal row 1, and on the vertebral row.

Geodipsas laphystia is distinguished from *G. boulengeri* and *G. zeny,* new species, by having more ventrals (170–187) and subcaudals (64–81) (<150 and <50, respectively, in both *boulengeri* and *zeny*) and by different color patterns (see species accounts). *Geodipsas laphystia* also reaches a larger size (>600 mm total length) than either *zeny* (maximum known length <300 mm), or *boulengeri* (maximum known length <400 mm).

Geodipsas laphystia has been confused with *G. infralineata,* but the two species differ most obviously in details of color patterns and more subtly in scale and

[2] See comment on the type locality for *Geodipsas zeny,* new species, described later, for notes on the name "Lalampo River."

[3] "Vevembe" was a word unknown to our guides from the Ranomafana National Park. We learned from questioning locals in the area that a rough translation is "big boundary" or "big fence" (the suffix *be* commonly means "big," "many," or "very" or, in some cases, takes on a meaning akin to "true"). "Vevembe" refers to the location of the forest roughly on the boundary between the Bara tribes to the west and the Taisaka people to the east.

Figure 1. Holotype of *Geodipsas laphystia* (MCZ 181390, male; total length 622 mm). The longitudinal lines distinguish this species from *G. infralineata* (Fig. 10).

hemipenial characters, body proportions, and size. In both species, the dorsal ground color is a shade of yellow to brown (or gray in *infralineata*), upon which is a series of fine dark lines. In *laphystia,* the lines form a series of dark longitudinal lines and flecks distributed as already described (Fig. 1). In *infralineata,* the lines form a lateral series of diagonals or fine chevrons pointed anteriorly (with the vertex on the vertebral scale row); successive lines or chevrons are usually separated by 2 scale rows (Fig. 10). In *laphystia,* the dorsal ground color does not encroach significantly onto the lateral edges of the ventrals, and the ventrals and subcaudals are immaculate except for a series of small midventral spots or a continuous midventral line that may be present on the posterior ⅔ of the body and on the subcaudals. In *infralineata,* the dorsal ground color may encroach substantially onto the ventrals, which may also be irregularly blotched or flecked with dark pigment in addition to having a midventral line or series of spots (Fig. 11).

Some specimens referred to *Geodipsas infralineata* apparently are nearly unicolor dorsally and lack distinct darker markings (whether longitudinal lines or diagonals). Although I did not observe this color form at any of the localities I worked, photographs of such specimens have appeared in Glaw and Vences (1994:pl. 336, from Andasibe) and Henkel and Schmidt (1995: 274, locality unknown). See additional comments in the account for *infralineata.*

Other characters distinguishing *Geodipsas laphystia* and *G. infralineata* include (1) differences in the mode of dorsal scale reductions (usually loss of row 4 or fusion of 4 + 5 in *laphystia,* fusion of 3 + 4 in *infralineata*); (2) details of hemipenial morphology (e.g., pair of large basal spines on the asulcate side in *laphystia,* parallel rows of greatly enlarged spines in *infralineata*; see Figs. 14, 17); (3) a somewhat longer tail and more subcaudals, on average, in *laphystia* (see Table 1); and (4) a greater body size in *infralineata* (to >900 mm total length) compared to *laphystia* (maximum known length 622 mm).

Data on the Holotype (MCZ 181390). The holotype is an adult male with fully everted hemipenes. Total length 622 mm; tail length 153 mm (24.5% of total length). Greatest head width (temporal region) 8.15 mm, head length 15.3 mm measured diagonally from tip of snout to end of mandibles. Dorsals in 19–19–17 rows, the reduction occurring by loss of row 4 at the level of ventral 126 (left) and fusion of rows 4 and 5 at the level of ventral 125 (right). One preventral (+ several small intergular scales), 181 ventrals, single anal plate, 81 pairs of subcaudals, 7–7 supralabials (3–4 touching eye), 9–9 infralabials, 1 + 2 temporals on each side.

Description. Measurements, proportions, and scutellation are summarized in Table 1; see also relevant sections later for descriptions of vertebral hypapophyses, skull, and hemipenis. Largest specimen the male holotype (MCZ 181390), 622 mm total length, 153 mm tail length; largest female (MCZ 181151), 608 mm total length, 132 mm tail length. Tail averaging 23% of total length in males, 21% in females.

Body slightly higher than wide and laterally compressed; ventrolateral edge of body angulate. Head distinctly wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior scale-row reduction nearly always by loss of row 4 or fusion of 4 + 5 at the level of ventrals 110–131 (N = 31 sides; by fusion of 3 + 4 on 1 side of 1 specimen). Ventrals 180–187 in males, 170–179 in females, usually preceded by 2 preventrals. Anal plate single. Subcaudals 70–81 in males, 64–71 in females.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials usually 9–9 (N = 13), less frequently 8–8 (4), 8–9 and 9–10 (2 each), and 7–8 (1); the first pair in contact behind the mental, usually 1–4 touching an anterior genial, 4–5 touching a posterior genial. Posterior genials approximately 1.6–1.8× as long as anterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 18–23 + 2 (N = 15); modal number of prediastemal teeth 19. Diastema broad, about 2–3× the width of the posteriormost solid maxillary tooth. The fangs are deeply grooved, about twice as large as the posteriormost solid teeth, and have a rounded anterior surface, a flattened knifelike posterior surface, and slightly compressed tips. The fangs are offset from the solid tooth row.

Hemipenis (See Fig. 14 and Detailed Description Later). Single (nonbilobed), noncapitate, acalyculate; proximally nude on the sulcate side, proximally spinose on asulcate side. Midsection bearing enlarged hooked spines on the sulcate and "lateral" sides; small spines on asulcate side. Distal tip spinulate. Sulcus spermaticus centrolineal, forked distally for about 30% of its length, the tips stopping short of the apex of the everted organ.

Coloration in Life. The dorsal ground color of *Geodipsas laphystia* is yellow to brown with dark brown or black lines and other markings superposed. Although smaller individuals *tend* to have lighter tones than larger individuals, no correlation of ground colors with size or sex is evident. Several small individuals of both sexes (MCZ 180341–43, 181148, 181152, 181158; snout–vent lengths [SVLs] 299–494 mm) had an overall yellowish ground color. My notes on other specimens describe the dorsal ground colors as pale yellowish brown (MCZ 180343; SVL 401 mm), medium brown (MCZ 180340; SVL 438 mm), or straw-colored (MCZ 180341; SVL 350 mm). Dorsal rows 1 and 2 are lighter than other dorsal rows.

The dark dorsal markings of *Geodipsas laphystia* (see Figs. 1, 3) consist of a series of longitudinal lines and flecks, but their distinctiveness and consistency vary. On most specimens, a line is present and continuous on the suture between dorsal rows 4–5 anteriorly (3–4 posteriorly). Less consistently, a line may be evident on the suture line between rows 7 and 8 (6 and 7 posteriorly). The border between the ventrals and dorsal row 1 usually has a series of darkened scale borders or a continuous (often wavy) line. Scattered scales in the vertebral row are edged with dark pigment, giving the impression of a linear series of dark flecks middorsally.

The head is usually of the same ground color as, or slightly lighter than, the dor-

→

Figure 2. Distributions of *Geodipsas laphystia*, new species, and *Geodipsas zeny*, new species. The type locality of *G. laphystia* is within the RNP; that for *G. zeny* is near Midongy du Sud (see text). Open symbol for *G. laphystia* is a literature record (see *Distribution*). The paratype of *G. zeny* from "Imerina" could be from any of the territory between roughly Andasibe and the RNP but more likely closer to the former; technically, the "Imerina country" referred to territory on the high plateau rather than on the eastern escarpment (see text). As explained in the text, *G. laphystia* could well be represented by some literature references to *G. infralineata*. Shaded area is above 1,000 m.

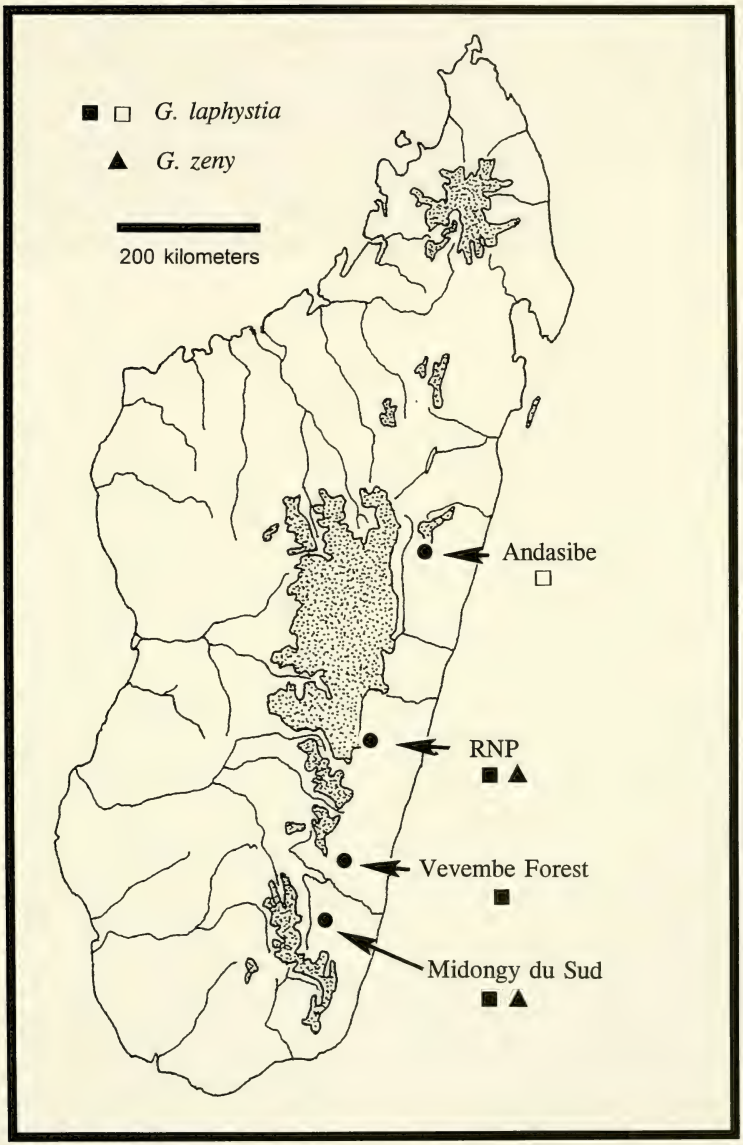
■ □ G. laphystia
▲ G. zeny
200 kilometers
Andasibe
□
RNP
■ ▲
Vevembe Forest
■
Midongy du Sud
■ ▲

TABLE 1. VARIATION IN MENSURAL AND MERISTIC CHARACTERISTICS OF MALAGASY SPECIES OF GEODIPSAS. MEAN ± SD ARE GIVEN FOR MEASUREMENTS AND COUNTS FOR *LAPHYSTIA, BOULENGERI* AND *INFRALINEATA* (*ZENY* AND *VINCKEI* REPRESENTED BY TOO FEW SPECIMENS). SEXES WERE NOT SEPARATED FOR *GEODIPSAS BOULENGERI* BECAUSE MOST AVAILABLE SPECIMENS OF THAT SPECIES WERE HATCHLINGS, FOR WHICH SEX WAS NOT VERIFIED. SAMPLE SIZES IN PARENTHESES.

	laphystia, new species	*zeny*, new species	*boulengeri*	*infralineata*	*vinckei* (holotype)
Dorsals	19–19–17	19–19–17	19–19–17[1]	19–19–17	21–19–17
Ventrals					
Males	182.8 ± 2.57 (10) 180–187	135–137 (2)	133.8 ± 1.92 (9) 131–137	186.7 ± 6.04 (10) 172–193	161
Females	173.8 ± 2.37 (12) 170–179	132 (1)	(sexes combined)	186.3 ± 8.38 (11) 173–199	
Subcaudals					
Males	76.7 ± 3.95 (10) 70–81	41 (2)	30.4 ± 4.56 (9) 24–36	71.3 ± 5.28 (8) 53–77	45
Females	66.9 ± 2.08 (10) 64–71	35 (1)	(sexes combined)	61.4 ± 4.83 (10) 53–68	
Maximum length (mm) (total [SVL])					
Males	622 (469)	281 (228)	353 (298)	783 (635)	493 (409)
Females	608 (476)	272 (230)	—	933 (765)	
Tail length/total					
Males	0.239 ± 0.009 (10) 0.23–0.26	0.18–0.19	0.14 ± 0.017 (9) 0.12–0.16	0.211 ± 0.020 (9) 0.17–0.23	0.17
Females	0.216 ± 0.005 (10) 0.21–0.22	0.15	(sexes combined)	0.188 ± 0.012 (10) 0.17–0.21	
Maxillary teeth	19.7 ± 1.23 (15) 18–23 + 2	15 + 2 (2)	16.3 ± 0.95 (10) 15–18 + 2	16.3 ± 1.18 (15) 15–18 + 2	18 + 2

[1] Two specimens were 18–19–17.

sum. A dark postocular streak extends from the posteroventral corner of the eye, across the upper edge of the supralabials and lower portion of the temporals, and ends at the corner of the mouth. A dark line extends from the posterior tip of the interparietal suture onto the nape or anterior neck. Otherwise, the top of the head usually has other dark flecks or small spots in an irregular pattern. The supralabials are pale yellow (brownish anteriorly), with an occasional darkened suture line. The infralabials and gular region are invariably immaculate pale yellow to white. The iris is yellowish brown to yellow. The tongue is pale yellow or flesh-colored with a blackish tip.

The ventral ground colors were usually pale yellow but occasionally dirty white. A series of dark flecks or spots is usually present midventrally on the posterior ⅔ of the body and on the tail, often discontinuous anteriorly or forming a continuous line posteriorly. Although occasionally evident nearly to the neck, these spots never reach the anterior ventrals or gular region. The extreme lateral edges of the ventral scutes are usually dusky, forming, with pigment on the lower edges of dorsal row 1, a dark line at the juncture of the ventral scutes with the dorsals.

Detailed color notes for a male (MCZ 181148) are as follows. Top of head yellowish with brownish wash. Brown median stripe extending from posterior end of parietals to 5–6 scale rows behind head. Brown postorbital stripe across upper edge of upper labials. A few tiny brown speckles on head scales behind prefrontals. Iris light yellowish brown. Dorsum brownish

Figure 3. *Geodipsas laphystia* (MCZ 181387; total length 595 mm). Specimen from the RNP.

yellow to yellow. Yellowish brown lateral stripe on rows 4–5. Brown flecks edge alternate paravertebral rows on most of body—on the tail these fuse into a very fine middorsal stripe. Venter of body and tail pale yellow. Midventral series of brown flecks beginning about ⅓ of way on body continue onto the first ½ of tail, 1 fleck per ventral scale. Similar series on border between ventrals and first scale row, becoming darker on edge of subcaudals. Upper and lower labials yellow.

Coloration in Preservative. Colors in preservative are similar to, but more subdued, than those in life: dorsal ground colors dull yellowish to brown, venter yellowish white to white. Dark markings brownish to blackish.

Until observing the hemipenial differences among sympatric samples of *Geodipsas infralineata* and *G. laphystia,* I had considered the subtle differences in color and pattern as intraspecific polymorphism. As indicated later, there is a great deal of variation in coloration and, to a lesser extent, pattern in *infralineata* (see *Coloration* in the *infralineata* species account). *Geodipsas laphystia* also is polymorphic in dorsal ground colors, although to a lesser extent than *infralineata.*

Natural History. All my observations suggest that *Geodipsas laphystia* is nocturnal and arboreal. Individuals are frequently encountered along small forest streams and rivers, probably in search of frogs and/or their eggs, which are the only recorded dietary items (see later). *Geodipsas laphystia* emits a foul-smelling secretion from the anal glands when handled.

Habitats of the 22 specimens I personally collected included undisturbed primary rainforest, forests slightly disturbed by old (≥50 years) selective logging, and riparian vegetation on floodplains and swamps associated with rivers and streams. I never encountered *Geodipsas laphystia* far from water (forest streams or rivers, flooded swamps, or pools). In view of the number of these snakes I personally observed and the diversity of microhabitats surveyed, their invariant association with water courses seems highly significant. Limited observations suggest that there may be some habitat segregation between *G. laphystia* and the very similar *G. infralineata.* Whereas no *G. laphystia* were found away from the edges of streams or pools, only occasionally were specimens of *G. infralineata* collected in association with water courses.

Most specimens of *Geodipsas laphystia* were found during or immediately after rains (or following periods of heavy rainfall), and all were collected from vegetation overhanging or immediately adjacent to streams or pools. Most specimens were 0.5–4 m up on woody or herbaceous vegetation overhanging water or were crawling among epiphytes on such vegetation. Typically, active *Geodipsas laphystia* were

encountered moving slowly in vegetation or else immobile, either in a loose irregular coil or stretched out; several were observed tongue-flicking the surfaces of leaves while crawling slowly in vegetation.

The body form of *Geodipsas laphystia* shows typical modifications associated with arboreality in colubrids (e.g., Guyer and Donnelly, 1990; Cadle and Greene, 1993). These include compression and attenuation of the body (shift of the center of gravity posteriorly), a long, narrow "neck," an angulate ventrolateral edge to the body, and a rather long, prehensile tail (Table 1).

Food records for *Geodipsas laphystia* obtained by palping freshly collected specimens were the following (N = 9 stomachs, one item per stomach except as noted): unidentified frog + eggs referred to *Mantidactylus luteus* (Ranidae; MCZ 181151, SVL 476 mm); *Boophis madagascariensis* (Rhacophoridae; MCZ 180340 and 180341, SVLs 438 and 350 mm, respectively), cf. *Boophis* sp. (Rhacophoridae; MCZ 181158, SVL 329 mm), cf. *Mantidactylus* sp. (Ranidae; MCZ 181393, SVL 467 mm), and egg clutches or egg clutches/hatching tadpoles of *Mantidactylus* spp. (Ranidae; MCZ 181387, SVL 458 mm; MCZ 181388, SVL 457 mm; MCZ 181389, SVL 435 mm; MCZ 181390, SVL 469 mm). These are supplemented by three field observations of consumption of frog egg clutches (details given below): *Mantidactylus luteus* (Ranidae; MCZ 180339 or 181164; SVLs 389 and 452 mm, respectively), *M. liber* (Ranidae; MCZ 180342, SVL 431 mm), and *M.* cf. *blommersae* (MCZ 181393; SVL 467 mm).

These records show that *Geodipsas laphystia* is a consumer of frogs and their eggs (especially *Mantidactylus* spp.). Many species of *Mantidactylus* attach their egg masses to leaves above flowing or standing water, and these may form a significant portion of the diet of *Geodipsas laphystia* during the rainy season when the egg masses are ubiquitous in montane and lowland rainforests where the species occurs. *Geodipsas laphystia* possibly also consumes eggs of other Malagasy frogs that deposit eggs in sites accessible to an arboreal snake, including many species of cophyline microhylids that lay eggs in tree holes.

Three instances of predation on frog eggs were observed in the field at Talatakely in the RNP. The following observations pertain to either MCZ 180339 (SVL 389 mm) or 181164 (SVL 452 mm) and were made on 6 December 1992 at the edge of a small temporary pond within rainforest (the two specimens were placed together in a collecting bag and the individual upon which the observations were based is uncertain). Many egg clutches of *Mantidactylus* spp. were attached to leaves around the pond. From 1950 to 2050 hours, the snake was stretched out along top of a large fern frond about 1 m above mud at the edge of the pond. On the frond, several clutches of *Mantidactylus luteus* eggs were suspended. During the hour of observation, the snake moved very slowly (30 cm maximum). I suspected the snake might be eating the frog eggs; one of the egg clutches appeared to have already been predated, as there was very little of it left. Eventually, the snake approached one of the clutches and rapidly moved its head back and forth through the clutch, opening and closing its mouth. Perhaps disturbed by light from my headlamp, the snake started to move away from the clutch, at which time it was collected. The snake was immediately palped and it regurgitated some of the milky egg clutch.

MCZ 181393 (SVL 467 mm) was observed on 30 December 1995 at the same pond as above, moving slowly and tongue-flicking along a grass stem 50–100 cm above the edge of the pond. Attached to the underside of leaves along this stem were clutches of *Mantidactylus* cf. *blommersae* eggs. After a few seconds, the snake approached one of the clutches and began consuming the eggs, biting through the clutch several times and then withdrawing.

MCZ 180342 (SVL 431 mm) was ob-

served on 2 January 1993 during a light drizzle on small tree branches about 3 m above a tiny rivulet in the forest. When first seen the snake had nearly finished consuming a clutch of *Mantidactylus liber* eggs attached to the top of a leaf. The snake was moving its head back and forth through the egg mass while at the same time opening and closing its mouth. No eggs appeared to be left in the clutch, although much of the jelly appeared to be intact.

Essentially nothing is known of the reproduction in any species of *Geodipsas*. Rather curiously, no females of any species that I personally collected, nor any museum specimens I examined by palpation, had eggs with enlarged yolks or shells. Two of eight adult females (SVLs 350–486 mm) of *G. laphystia* that I collected had evidence of early vitellogenesis (follicles 2–3 mm diameter; follicles of all other specimens ≤1 mm); reproductive condition was not examined for museum specimens. The two vitellogenic females (MCZ 181159 and 181393) were collected on 13 January 1993 and 30–31 December 1995; dates of collection for the nonvitellogenic females were 4 December to 1 January. Given the absence of vitellogenic females earlier in the rainy or dry season, it seems plausible that *G. laphystia* lays eggs well into the rainy season (i.e., February–April) in the southern portion of the eastern rainforest belt. This is somewhat later than several sympatric species of *Liopholidophis* (Cadle, 1996), and may reflect the fact that the period of major annual activity for *Geodipsas laphystia* appears to coincide with the beginning of the rainy season (usually the last half of December), whereas species of *Liopholidophis* are active much earlier (Cadle, 1996). It may require females of *G. laphystia* some time to acquire sufficient fat stores to initiate vitellogenesis after the rainy season begins. Some circumstantial evidence suggests that sexual maturity of males may occur at approximately 300–350 mm SVL (see *Remarks*).

Remarks. Primarily in conjunction with ascertaining the sexual maturity of the male types of *Geodipsas zeny*, new species, to be described next (see *Remarks* for that species), I examined spine mineralization in hemipenes of a size series of *Geodipsas laphystia* by clearing and staining with alizarin (alizarin binds to mineralized tissues, including hemipenial spines, permitting easy visualization of the extent of mineralization). Annecdotal observations, primarily of Charles W. Myers (personal communication), had suggested a general relationship between hemipenial spine mineralization and other gross indications of sexual maturity. These observations included the presence of nonmineralized or weakly mineralized spines in snakes lacking other indications of maturity (e.g., convoluted vasa deferentia, anal ridges) and well-mineralized spines in mature snakes.

I cleared and alizarin-stained one everted hemipenis from each of three specimens of *Geodipsas laphystia*: MCZ 181148 (SVL 299 mm), MCZ 181152 (SVL 360 mm), and MCZ 180342 (SVL 431 mm). In *G. laphystia*, enlarged, curved spines protrude from the midsection of the hemipenis, and these grade distally into long straight spinules; a pair of enlarged spines is present basally on the asulcate side (see detailed hemipenial description, later). Upon inspection under a dissecting microscope, neither the hemipenial spines nor spinules of MCZ 181148 seemed to be mineralized (at most, only very slightly mineralized), whereas those of the other two specimens were well mineralized. The staining revealed that in MCZ 181148 the protruding portions of the enlarged hooked spines on the midsection of the organ and at the base of the asulcate side were mineralized, but none of the elongate spinules on the distal portion, nor the smaller spines of the body, were. All spines and spinules of the other two organs were well mineralized.

A general correspondence of spine mineralization with other signs of reproductive maturity seems to hold. MCZ 181148 has

small, poorly differentiated testes and nonconvoluted vasa deferentia, indicating sexual immaturity. Both of the other specimens have large, compact testes obviously packed with coiled tubules, and convoluted vasa deferentia (those of MCZ 181342 more convoluted than in MCZ 181152). Thus, a general relationship between hemipenial spine mineralization and sexual maturation in *Geodipsas laphystia* is corroborated, although much more work needs to be done to quantify that relationship further.

This exercise also permitted some observations on the ontogeny of spine mineralization. In MCZ 181152 and 181342, both of which have fully developed spines, the clearing and staining revealed that each of the enlarged spines has a broadened base just under the surface of the organ and a long spur extending distally from the base through the soft tissue of the organ. The spinules have no such broadened base or spur, their internal portion being the same diameter as the protruding portion. There is a gradual transition in the morphology of the hidden, basal portion of these ornaments from the enlarged spines on the midsection to the elongate distal spinules (a similar gradual transition occurs in the visible external portion). By comparison, in MCZ 181148 only the external, protruding portion of the spines and a small, unexpanded portion of the internal base are mineralized. This suggests that mineralization proceeds from external to internal, at least for the enlarged spines on the midsection.

An unanswered question is whether mineralization of the distal spinules occurs relatively rapidly with the onset of sexual maturity or the transition is more gradual. Whereas there is no apparent difference between MCZ 181152 and 181342 (70 mm difference in body size) in the extent of spine mineralization other than general size increase, the difference between MCZ 181148 and 181152 (60 mm difference in body size) is striking. This suggests that, at least for the distal spinules and the internal portions of the enlarged midsection spines, onset of extensive mineralization, and perhaps sexual maturity, may occur relatively rapidly at a body size of approximately 300–350 mm.

The suggestion that hemipenial spine mineralization may indicate sexual maturity should be more carefully investigated in snakes, but also in other squamates. For example, some varanid lizards have mineralized "hemibacula" in their hemipenes (Card and Kluge, 1995). Card and Kluge (1995) found no seasonal variation in mineralization of those elements. For *Varanus gouldii,* they also reported that the hemibacula remain unmineralized for at least up to a year posthatching. The implication is that the hemibacula may mineralize coincident with sexual maturity in these lizards, as already suggested for snake hemipenial spines. Thus, extensive mineralization of hemipenial elements may be an indicator of male maturity in those squamates having such elements as adults.

Geodipsas zeny, new species

Figures 4–6; Table 1

Holotype. Museum of Comparative Zoology, Harvard (**MCZ**) **181161** (JEC 12580), an adult male in good condition (Figs. 4, 6). Specimen collected 11 January 1993 by John E. Cadle.

Type Locality. Approximately 7 km SW (airline) Midongy du Sud [Midongy Atsimo], near Rianambo ("high waterfall") on Lalampo River, 670 m elev., Fivondronana Midongy du Sud, Prov. Fianarantsoa, Madagascar [23°39′S, 46°57′E].

Paratypes. **MCZ 181162** (JEC 10124), female, apparently adult (see *Remarks*), 6 December 1990: Talatakely (at the village of Ambodiamontana), Ranomafana National Park, 980 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°16′S, 47°25′E]. Collected by a villager.

The Natural History Museum, London (BMNH) 95.10.29.62 (Figs. 5, 6), adult male from "Imerina, Madagascar" obtained by the Reverend R[ichard] Bar-

Figure 4. Holotype of *Geodipsas zeny* (MCZ 181161, male; total length 281 mm) from near Midongy du Sud.

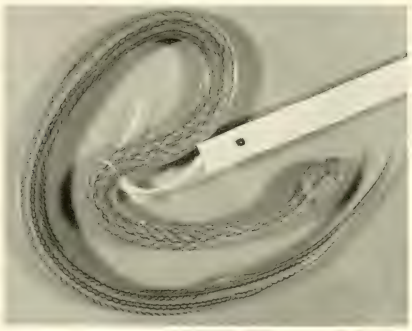

Figure 5. Paratype of *Geodipsas zeny* (BMNH 95. 10. 29. 62, male; total length 266 mm) from "Imerina, Madagascar."

on, probably in the early 1890s. The descriptor "Imerina" refers to the territory occupied by the indigenous people of that name in the central plateau between approximately parallels 18° and 21° (see, e.g., Gallieni, 1908:pl. 6).

Comment on the Type Locality. In field notes and in previously published work (Cadle, 1996:460–461; localities for *Liopholidophis infrasignatus, L. lateralis,* and *L. sexlineatus*), I originally transcribed the name "Lalampo River" as "Alapo River" based on my interpretation of local informants' pronunciation. Here I correct the name to "Lalampo" following the 1:100,000 "Befotaka" map published by the Institute Géographique National, Paris (1961; available through the Foiben-Taosarintanin'i Madagasikara [FTM], Antananarivo). Neither name appears in recent gazetteers (e.g., Defense Mapping Agency, 1989). Given my original field transcription, it may be referred to locally as any of the variants "Lalampo," "Alampo," or "Alapo." As of 1996, a 1:50,000 topographic map of the area was unavailable to verify the name. The Lalampo is a tributary of the Itomampy River, which is the major river flowing through the town of Midongy du Sud.

Upstream from the type locality, the river passes over a high precipice and has eroded down to bedrock, forming a waterfall that is a well-known local landmark. *Rianambo* is a compound word from the Malagasy *riana* (= waterfall) + *ambo* (= big or high). From the top of the falls I recorded a compass reading of 63° to the town of Midongy du Sud, visible in the distance, thus making the waterfall and our campsite approximately 243° in a southwesterly direction from the town.

Distribution (Fig. 2). The two known localities are approximately 270 km apart in the southern portion of the eastern rainforest belt of Madagascar. The BMNH specimen with imprecise locality most likely came from the eastern, forested portion of the Imerina territory in central Madagascar. The known elevational range of *Geodipsas zeny* is 670 m at the type locality to 980 m at the other precise locality. The types are the only known specimens.

Etymology. The specific epithet, *zeny* (pronounced approximately as zeh' -nē), used here as a noun in apposition, is a Malagasy word meaning "dwarf" or "dwarfish." It refers to the diminutive size of *G.*

zeny in comparison to other Malagasy *Geodipsas*.

Diagnosis. Geodipsas zeny is smaller (maximum known total length 281 mm) than other described species of Malagasy *Geodipsas* (maximum known total lengths ≥447 mm) and has the following distinguishing features: low number of ventrals (132–137) and subcaudals (35–41); a bold dark gray midventral line from the neck to the vent (Fig. 6); paired dark nape blotches or a dark collar; and dark borders to the dorsal scales that tend to form a reticulated network or dark diagonals on the flanks anteriorly and dark longitudinal streaks posteriorly.

Geodipsas zeny is essentially indistinguishable from *G. boulengeri* in the usual scutellational features that distinguish snake species (e.g., ventral, subcaudal, dorsal counts). Prior to examining specimens of *G. "heimi"* (= *boulengeri*, as shown later), I had considered specimens of *zeny* possibly as that species solely on this basis (*zeny* will key to *"heimi"* using the key to species in Glaw and Vences [1994]). However, *G. zeny* differs from *boulengeri* in several coloration/pattern differences, including the following (contrasting characters of *boulengeri* in parentheses): (1) a thick, bold midventral dark gray line extending from the neck or anterior body to the vent (venter without continuous, bold midventral line; usually immaculate, but occasionally with a midventral series of scattered small dots); (2) a pair of dark nape blotches that may be connected by dark pigment to form a continuous collar (paired light neck blotches behind the jaw angle); (3) a dark streak from the posterior edge of the frontal scale to the nape along the parietal suture (no dark streak on parietal suture); (4) dark borders of dorsal scales tending to form a fine network or diagonals anteriorly, forming indistinct dark streaks on rows 3–4 and 6–7 posteriorly (dark network present or not, and not forming streaks posteriorly); and (5) light areas on labial scales not forming discrete spots and not bordered by a discrete dark line (light spots discrete, though often irregularly shaped, and bordered by a discrete narrow dark line). In addition, *zeny* differs from *boulengeri* in hemipenial characters, including fewer spines around the midsection, a more divided sulcus, and absence of a basal lobe.

Geodipsas zeny differs from *G. infralineata* (contrasting conditions in parentheses; see Table 1) by its smaller size (to >900 mm total length), fewer ventrals (172–199) and subcaudals (53–77), and shorter tail (17–23% of total length), and in hemipenial morphology (see descriptions later; Figs. 15, 17). Many specimens of *G. infralineata* have a midventral dark line, but it is usually narrow and anteriorly incomplete, in contrast to the bold thick midventral line that is complete from the neck to the vent in *zeny*. Some specimens of *infralineata* resemble *zeny* in having paired dark nape blotches and a dark streak along the parietal suture (Figs. 10, 12). Virtually the same characters that distinguish *zeny* from *infralineata* also distinguish *zeny* from *laphystia* (see Table 1 and diagnosis of *G. laphystia*).

Geodipsas zeny differs from *G. vinckei* (known only from the holotype; characteristics in parentheses) in having fewer ventrals (161) and in color pattern (light collar on nape; anterior ventrals with dark anterior border, resulting in a ladderlike pattern; posterior ventrals with triangular or halfmoon–shaped dark blotches).

Data on the Holotype (MCZ 181161). The holotype is an adult male with fully everted hemipenes (the left one removed for illustration; Fig. 15). Total length 281 mm; tail length 53 mm (19% of total length). Greatest head width (temporal region) 5.5 mm, head length 11.1 mm measured diagonally from tip of snout to end of mandibles. Dorsals in 19–19–17 rows, the reduction occurring by loss of row 4 at the level of ventrals 95 (left) and 98 (right). Two preventrals, 135 ventrals, single anal plate, 41 pairs of subcaudals, 7–7 supralabials (3–4 touching eye), 9–9 infralabials, 1 + 2 temporals on each side.

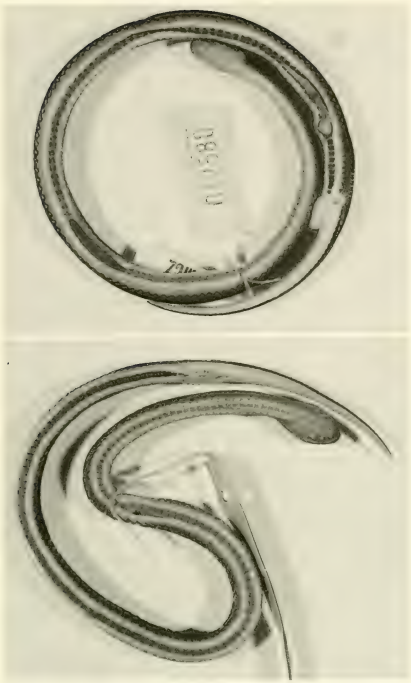

Figure 6. Ventral views of the holotype (top; MCZ 181161) and male paratype (bottom; BMNH 95. 1. 29. 62) of *Geodipsas zeny*. The wide midventral stripe extending the length of the body appears to be diagnostic of this species (cf. *Geodipsas infralineata*, Fig. 11).

Description. Measurements, proportions, and scutellation for the 3 known specimens are summarized in Table 1; the specimens are identified in the following description as "MCZ" and "BMNH" unless individual identity is necessary. Largest male (MCZ 181161), 281 mm total length, 53 mm tail length; female, 272 mm total length, 42 mm tail length. Tail length 18–19% of total length in males, 15% in female. Body slightly higher than wide; ventrolateral edge of body angulate. Head slightly wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior dorsal scale reduction by loss of row 4 at the level of ventrals 91–105 (N = 5 sides). Ventrals 135–137 in males, 132 in female; preceded by 1 or 2 preventrals. Anal plate single. Subcaudals 41 in males, 35 in female.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials 7–9, the first pair in contact behind the mental, 1–4 (MCZ specimens) or 1–3 (BMNH) touching an anterior genial, 4–5 (MCZ) or 3–4 (BMNH) touching a posterior genial. Anterior genials shorter than (MCZ 181161, BMNH) or approximately equal to (MCZ 181162) posterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 15 + 2 (N = 2). Diastema about 1.5–2× the width of the posteriormost solid maxillary tooth. The fangs are deeply grooved, about twice as large as the posteriormost solid teeth, and have a rounded anterior surface, a flattened knifelike posterior surface, and slightly compressed tips. The fangs are offset from the solid tooth row.

Hemipenis (See Fig. 15). Single (nonbilobed), noncapitate, acalyculate; proximally nude, with a spinose midsection, and distally spinulate. Distal ornamentation sharply set off from that of the midsection, resulting in a rather distinct head region. Sulcus spermaticus centrolineal and forked distally for approximately 15% of its length.

Coloration in Life (MCZ 181162). Dorsum dark brown, somewhat iridescent, with tiny scattered dark punctations forming a fine reticulated network over most of body, indistinct lines posteriorly. Top of head dark brown, with dark brown longitudinal line from posterior edge of frontal to nape. An indistinct dark brown postocular bar is present. Upper and lower labials dusky grayish brown. Throat grayish brown with some whitish punctations.

Outer edges of ventrals dusky grayish brown; center part of each ventral with a squarish dark brown blotch, giving impression of broad midventral dark brown stripe (approximately ¼ the width of the ventral scutes). Portion of ventrals between center blotches and lateral edges is whitish with grayish brown irregular markings. Subcaudals whitish, with midventral dark line. A very indistinct lighter stripe (brown with very thin darker border) is present on extreme posterior body, continuing onto tail (evident only on close inspection).

Coloration in Preservative. MCZ 181161–62 are dark brown dorsally with a fine network of very dark brown/blackish markings over the entire body, tending to form narrow diagonals anteriorly and longitudinal lines posteriorly (Fig. 4). BMNH 95.10.29.62 has a lighter grayish brown ground color with similar dark markings (Fig. 5). Top of head medium brown with dark brown markings. The venter is dirty white and the midventral stripe is dark gray to medium brown. The dorsal pigment encroaches as fine stippling laterally onto the ventral plates, where it forms a narrow border (MCZ 181161, BMNH 95.10.29.62) or more extensive coverage toward the midline (MCZ 181162).

The head bears a dark brown line from (and including) the posterior edge of the frontal, narrowly bordering the interparietal suture, and connecting to the neck collar (MCZ specimens) or ending on the neck just posterior to a pair of nape blotches (BMNH). Top of head otherwise with a complex marbled pattern composed of various shades of brown, black, and gray. An indistinct dark brown postocular stripe occupies the ventral edges of the temporals (most discrete in the holotype, less so in MCZ 181162, and not evident in the BMNH specimen). Upper labials whitish, heavily speckled with dark gray or brown, with unpigmented areas forming discrete spots in the holotype and BMNH specimen, but not in MCZ 181162. A dark brown nape collar 2–3 scales wide is present in the MCZ specimens; it broadens laterally to give the appearance of a blotch on either side of the neck and extends ventrally to the mouth line. In the BMNH specimen the nape collar is interrupted middorsally so this specimen appears to have a pair of nape blotches (Fig. 5). Infralabials and gular region finely peppered with dark gray infralabials with discrete white spots in BMNH 95.10.29.62, less discrete in MCZ 181161, and not apparent in MCZ 181162. Gular region peppered with dark gray, but having indiscrete irregular light areas (most distinct in BMNH 95.10.29.62).

Dorsum with complex network of dark brown/black, forming posteroventrally slanting diagonal lines anteriorly that occur along suture lines every second dorsal scale row (Figs. 4–5). On the posterior ½–⅔ of the body, the network tends to fuse into lines. At about midbody, these lines are on the suture line and/or adjacent areas of rows 4–5 and 6–7 (posteriorly 3–4 and 5–6) and on the middorsal scale row, in which each scale is outlined with dark pigment but has a light center. The posterior lines are not so evident in MCZ 181162 as in the other specimens, and they are evident much farther anteriorly in BMNH 95.10.29.62 than in MCZ 181161. The lines continue to the tail tip, tending to fuse with one another on the tail.

The midventral dark stripe is composed of a series of bold, squarish blotches with more or less regular edges, one in the center of each ventral plate (Fig. 6). These align to form a broad midventral stripe extending from just behind the head to (and including) the anal plate (Fig. 6). Under magnification the midventral stripe is seen to be composed of a very dense fine stippling. Anteriorly the stippling is less dense and the overall appearance of the stripe lighter than posteriorly. BMNH 95.10.29.62 has a short, thin, dark line on the ventral surface of the proximal portion of the tail; MCZ 181162 has a similar line extending about ⅗ the tail length; and in MCZ

181161 the ventral surface of the tail is immaculate.

Natural History. The holotype was collected while active at night 2 m aboveground in a shrub at the edge of a flooded, meadowlike, vegetation-choked bog (with grasses and ferns up to about 1.2 m high) in riparian forest. Many frogs were calling at the site, including *Scaphiophryne marmorata* (Microhylidae), *Mantidactylus liber* and *Ptychadena mascareniensis* (Ranidae), *Heterixalus betsileo* (Hyperoliidae), and *Aglyptodactylus madagascariensis* and *Boophis granulosus* (Rhacophoridae). MCZ 181162 was collected while active on a trail in moderately disturbed forest at about 0730 hours. These two observations do not permit any general statement about daily activity patterns of *Geodipsas zeny* (of the other species of *Geodipsas* occurring in the RNP, *G. infralineata* and *G. laphystia* apparently are nearly exclusively nocturnal, whereas the only specimen of *G. boulengeri* from the park was collected during the day).

Similarly, with so few observations it is difficult to speculate on the usual macrohabitat (arboreal, terrestrial, cryptozoic; see Cadle and Greene, 1993) of *Geodipsas zeny.* Although the type was collected from a small tree, the body form of *G. zeny* shows few clear modifications associated with arboreality. Nevertheless, the ventrolateral edge of the body is angulate, a character often, but not invariably, associated with arboreality in snakes. However, the short body and tail and the lack of body compression and attenuation suggest a terrestrial snake.

Geodipsas zeny is broadly sympatric with *G. infralineata, G. laphystia,* and *G. boulengeri* in the RNP and with at least *infralineata* and *laphystia* at the type locality. Both *G. zeny* and *G. boulengeri* were the least commonly encountered colubrids in the RNP survey (one specimen each over several long field expeditions).

Remarks. All three specimens of the type series are small snakes and it might be questioned whether they are adults. Sexual maturity is indicated in the two males by well-mineralized hemipenial spines and spinules, by convoluted vasa deferentia, and by the convoluted surface of the kidneys, which indicates secretory activity of the sexual segments of the renal tubules (e.g., Fox, 1952; Myers, 1965). To a first approximation, a general correlation between the extent of hemipenial spine mineralization and sexual maturity seems to hold for *Geodipsas laphystia* (see *Remarks* for that species). Assuming that the same general pattern holds for *G. zeny,* sexual maturity of the males of *zeny* is indicated by the mineralization of *both* the enlarged spines and (especially) the spinules on the distal end of the organ.

Sexual maturity of the female paratype of *Geodipsas zeny* is suggested by enlarged and slightly convoluted oviducts, which are about as convoluted as those of some apparently mature *G. infralineata* and *G. laphystia.*

The female of *Geodipsas zeny* is approximately the same size as the two known males, which suggests little sexual size dimorphism in this species. Nevertheless, given the small sample size it would be premature to make firm conclusions. Of the other species of *Geodipsas* for which I have examined adequate samples ($N > 20$ individuals), *G. laphystia* shows no evidence of strong sexual dimorphism (largest specimen a male; Table 1), whereas *G. infralineata* shows the usual colubrid pattern wherein females reach larger body sizes than males (Table 1).

SYNONYMY OF *TACHYMENIS BOULENGERI* PERACCA AND *GEODIPSAS HEIMI* ANGEL

Peracca (1892) described *Tachymenis* (now *Geodipsas*) *boulengeri* on the basis of a single adult male (Museo Regionale di Scienze Naturali, Torino [MZUT] 1874; see Figs. 7–8) from near Andrangoloaka (19°02′S, 47°55′E; Fig. 9; see Cadle [1996: 401] for discussion of this locality). Mocquard (1894) described *Compsophis albi-*

ventris, new genus and species, on the basis of a single juvenile (Muséum National d'Histoire Naturelle, Paris [MNHN] 1893.212) from Montagne d'Ambre (= Ambohitra, Antsiranana Province; 12°30′S, 49°10′E; Fig. 9 [star]). Angel (1936) described *Geodipsas heimi* on the basis of an adult male (MNHN 1936.19) from near Tsianovoha (= Tsianovoho, Fianarantsoa Province; 21°57′S, 47°21′E; Fig. 9). *Geodipsas boulengeri* and *Compsophis albiventris* have been recognized only from the type specimens until the additional specimens of *boulengeri* reported herein. *Geodipsas heimi* has been reported from the type locality and from the vicinity of Montagne d'Ambre at the northern tip of Madagascar (Raxworthy and Nussbaum, 1994; Glaw and Vences, 1994; *Specimens Examined*). Several authors (e.g., Brygoo, 1983; UICN, PNUE, and WWF, 1990; Glaw and Vences, 1994) have expressed uncertainty as to whether or not *boulengeri, albiventris,* and *heimi* represent distinct taxa, but the problem has not received detailed attention. I have had the opportunity to simultaneously compare the holotypes of all three nominal taxa.

The relationship of *Compsophis albiventris* to the other two taxa is complicated by the interpretation of dentitional variation that is currently under study; it will be considered in a separate report. Nonetheless, that complication does not preclude, for the present, an assessment of whether *boulengeri* and *heimi* represent the same taxon. Because my immediate goal is to assign a name to the Ranomafana population, and because *boulengeri* is the earliest available name involved, the eventual fate of *C. albiventris* relative to the other two taxa has no bearing on the species designation applied to the RNP population. Thus, I set aside for later consideration the relationship of *Compsophis albiventris* to the other nominal taxa here under discussion.

The taxonomic status of *heimi* vis-à-vis *boulengeri* is relatively straightforward. Angel (1936) considered *G. heimi* "very close" to *G. boulengeri.* The type localities of *Tachymenis boulengeri* and *Geodipsas heimi* are approximately 335 km apart on the eastern escarpment. A single specimen referred to *boulengeri* (*Specimens Examined*) is known from the RNP, a locality between the two type localities (Fig. 9). Basic meristic and mensural data on the types of these taxa are given in Table 2; original descriptions of the type specimens are good (*heimi*) to excellent (*boulengeri*). As shown in Table 2, the types of *boulengeri* and *heimi* are very similar. The major difference is the point of posterior dorsal scale-row reduction, but the difference between the two types is the sort of range observed intraspecifically in many colubrids. Angel (1936) noted as additional differences between *heimi* and *boulengeri* "head plates of different dimensions," a longer tail in *heimi,* a single (*heimi*) versus double (*boulengeri*) loreal, and "coloration." Angel apparently was referring to the frontal plate dimensions for the first character ("twice as long as wide" in *boulengeri* [Peracca, 1892:3], and "1⅓ as long as wide" in *heimi* [Angel, 1936:127]); these are minor differences, especially considering that no estimations of variance in this character are available. Likewise, relative tail proportions are very similar in the two types (Table 2). The loreal and coloration characters require more extended discussion.

In the holotype of *boulengeri,* each loreal is divided into a small superior portion, ¼ to ⅕ the size of a larger inferior portion. The supernumerary scales are well formed in each case and appear as the sort of normal variation seen in, for example, divisions of circumorbital head plates in many colubrids (e.g., the divided postocular on one side of the type of *boulengeri*; cf. Table 2). The holotype of *boulengeri* is the only specimen examined that had a divided loreal, and this variant seems to be less common in colubrids than divisions of other lateral head plates. Nonetheless, it seems a rather minor difference upon which to base a species distinction, given

Table 2. Meristic and mensural characteristics of the holotypes of *Tachymenis boulengeri* Peracca and *Geodipsas heimi* Angel.

	Tachymenis boulengeri Peracca, 1892 MZUT 1874	*Geodipsas heimi* Angel, 1936 MNHN 1936.19
Sex	male (adult)	male (adult)
Length		
Total	329 mm	352 mm
Tail	48 mm	55 mm
Tail/total	0.14	0.16
Dorsal scales	19–19–17	18–19–17
Ventral scales	135 (+2 preventrals)	132 (+3 preventrals)
Posterior scale		
Reduction (L/R) (ventral scale position)	−4 (104)/3 + 4 (108)	−4 (87)/−4 (91)
Subcaudal scales	31	34
Preocular scales	1–1	1–1
Postocular scales	3–2	2–2
Temporal scales	1–1, 2–2	1–1, 2–2
Labial scales		
Upper (bordering eye)	7–7 (3–4)	7–7 (3–4)
Lower	8–9	9–8
Maxillary teeth	15 + 2	17 + 2

other strong and unusual similarities (Table 2).

As for coloration, the types of both *boulengeri* and *heimi* were reported as having a generally brown dorsum and a "brilliant yellow" (*heimi*; Angel, 1936) or "orangish yellow" (*boulengeri*; Peracca, 1892) venter, an unusual pattern of yellow to orange blotches on the side of the neck, and yellowish spots on the supra- and infralabials and gular scales (Fig. 8). Both Angel and Peracca were undoubtedly describing the coloration of preserved specimens, so any differences in coloration could easily reflect preservation methods and the amount of time in preservative. The type of *heimi* has a median ventral series of small irregular dark punctations from the neck to the vent that is absent in the type of *boulengeri*.

Comparison of coloration of the types of *boulengeri* and *heimi* now is difficult because of considerable darkening of the type of *heimi*; it is presently rather dessicated and very dark brown dorsally and dirty gray ventrally. The labial spots and nape blotches are still evident but are dirty gray. Except for fading of the ventral color, the type of *boulengeri* is much as Peracca described it and is more or less the same color as a recently collected specimen referred to *boulengeri* from the RNP (MCZ 181163, preserved in 1990).

Despite preservational differences, several aspects of the dorsal and head patterns shared by the types of *Geodipsas boulengeri* and *G. heimi* are so unusual as to make it virtually certain that these are the same taxon. All of these features are also observed in the RNP specimen assigned to *boulengeri* (*Specimens Examined*). They are (see Figs. 7–8) (1) rounded, light spots on the supra- and infralabial scales, each with a dark border; (2) a pair of large, light, curved spots on the neck behind the angle of the mouth; (3) a dusky gular region with irregular light spots; and (4) light dark-bordered flecks on many dorsal scales (these are obscured by general darkening of the type of *heimi* but are still visible under close scrutiny).

The left hemipenis of the holotype of *Geodipsas heimi* was studied superficially *in situ*, and then everted by the method of Pesantes (1994) and compared with the everted organ of the specimen of *G. bou-*

lengeri from Ranomafana (MCZ 181163; described later; see Fig. 16). The organs are essentially identical insofar as general structure and details of ornamentation.

Given that the holotypes of *Tachymenis boulengeri* Peracca and *Geodipsas heimi* Angel are exceedingly similar in scutellation, body proportions, maxillary dentition (Table 2), and hemipenial morphology, and share highly unusual features of coloration, I interpret the double loreals of the type of *boulengeri* as an unusual scutellational variant, but not a substantive indication of distinct taxa. Hence, *Geodipsas heimi* Angel (1936) is synonymized with *Tachymenis boulengeri* Peracca (1892).

Key to Species of *Geodipsas* in Madagascar

I recognize six species of *Geodipsas* in Madagascar: *boulengeri* Peracca, *infralineata* Günther, *laphystia* Cadle, *vinckei* Domergue, *zeny* Cadle, and a species referred to herein as *Geodipsas* species inquirenda. This last species, of which all known specimens are from the vicinity of Montagne d'Ambre in northern Madagascar (*Specimens Examined*), is discussed in the species account for *Geodipsas boulengeri*. Final determination of its status will be considered in a separate report dealing with the status of *Compsophis albiventris* Mocquard, which is known only from the same locality. The following key should allow identification of all species of *Geodipsas* in Madagascar. Because of small sample sizes, the ventral scale character used in couplet 3 may, in fact, overlap between the two species when more specimens are examined.

1. Fewer than 155 ventrals and fewer than 45 subcaudals. Body rounded 2
   More than 155 ventrals and 45 or more subcaudals. Body strongly compressed[1] 4
2. Bold dark gray or brown midventral line from the neck to the vent; large dark brown spot on each side of the nape or a dark collar. If light areas are present on labial scales, they do not form discrete spots ..... *Geodipsas zeny* Cadle
   Midventral line, if present, not bold: at most, an interrupted series of small dots, present mainly on posterior body. A large, single *light* spot on neck behind the jaw angle; light areas on labials form discrete (though often irregular) spots surrounded by a dark line 3
3. Fewer than 140 ventrals (131–137 in 9 specimens). Gular region dusky with light spots. Light spots on supralabials small (covering much less than ¼ of each scale), rounded, not reaching the labial border. Spots on neck behind the jaw angle at least 2 scales wide at broadest point. Gular regions dusky with irregular light areas. Discrete light flecks on many dorsal scales ..... *Geodipsas boulengeri* (Peracca)
   More than 140 ventrals (143–150 in 5 specimens). Gular region immaculate (light). Light supralabial spots larger (some covering ¼ or more of each scale), elongate or irregular, and at least some reaching the labial border. Spots on neck behind the jaw angle 1 scale or less in width at the widest point. Gular region immaculate. Discrete light flecks on dorsals usually absent (when present, on few dorsals only) ..... *Geodipsas* species inquirenda (Montagne d'Ambre region only)
4. No light collar on posterior part of head and on nape. Venter more or less immaculate or with a midventral line (especially posteriorly), interrupted or not; lateral encroachment of dorsal pigment onto ventrals, and other irregular ventral spotting may be present. Subcaudals >50. Two postoculars 5
   Light collar across temporal region and nape. Each ventral scute with a transverse dark marking along its anterior edge, forming a ladder-like pattern. Subcaudals 45 and 3 postoculars in only known specimen ..... *Geodipsas vinckei* Domergue
5. Dorsal pattern including a series of fine, dark *chevrons or diagonals* (rarely unicolor) on a highly variable ground color (dark gray, brown, grayish brown, or yellowish). Posterior scale reduction usually by fusion of rows 3 + 4 *Geodipsas infralineata* (Günther)
   Dorsal pattern including a series of fine, dark *longitudinal* lines (on anterior body on suture lines and adjacent scales between rows 4 and 5, 7 and 8, and/or the border between the ventrals row 1; sometimes on vertebral row). Ground color variable (grayish, brownish, or yellowish). Posterior scale reduction usually by fusion of rows 4 + 5 ..... *Geodipsas laphystia* Cadle

[1] Equivocal in *Geodipsas vinckei*, as noted in the diagnosis of *G. infralineata*.

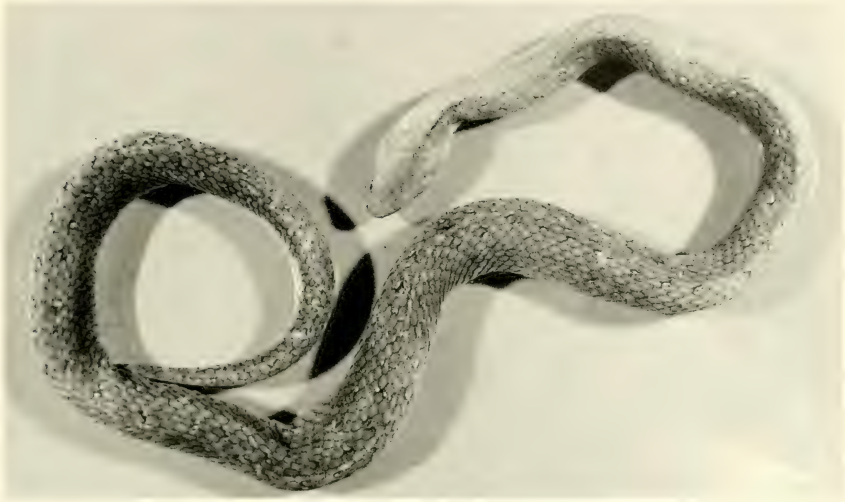

Figure 7. Holotype of *Tachymenis boulengeri* Peracca (MZUT 1874; total length 329 mm).

SUMMARY OF TAXONOMIC AND NATURAL HISTORY DATA FOR *G. BOULENGERI* AND *G. INFRALINEATA*

In addition to *Geodipsas laphystia* and *G. zeny, G. boulengeri* and *G. infralineata* are known from the RNP. Here I summarize variation in taxonomic characters for these two species and aspects of their natural history and behavior. The other two species, *G. vinckei* Domergue and *Geodipsas* species inquirenda, are not known from the RNP. *Geodipsas vinckei* is known only from the type specimen from Andasibe (Domergue, 1988). *Geodipsas* species inquirenda is known from specimens referred to *G. heimi* (= *boulengeri*) from the vicinity of Montagne d'Ambre. As discussed later (species account for *G. boulengeri*), these specimens are not conspecific with *boulengeri*. The distributions of all of these species are shown in Figure 9.

Geodipsas boulengeri (Peracca) Figures 7, 8; Tables 1, 2

Tachymenis boulengerii Peracca, 1892:3–4, Figs. 2*a–d* (type locality, "Valle dell'Umbi (Andrangoloka)"

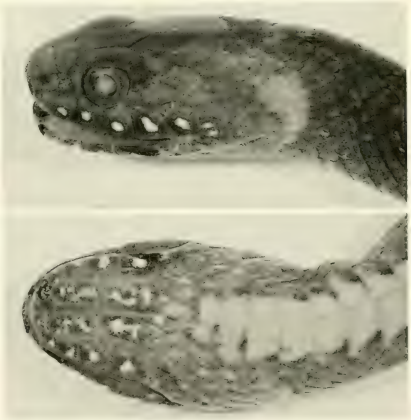

Figure 8. Head of the holotype of *Tachymenis boulengeri* Peracca (MZUT 1874) in dorsolateral and ventral views. Diagnostic features visible include the light postmandibular spot, light spotting on upper and lower labials, and dusky gular region with irregular light spotting.

[Valley of the Umbi River (Andrangoloka)] [= Andrangoloaka; 19°02′S, 47°55′E; Fig. 9]. Holotype, MZUT 1874 (Figs. 7–8). Mocquard, 1909:47. Cadle (1996:401) discussed the type locality and the collection from which the type came.

Geodipsas boulengeri (Peracca): Boulenger, 1896:32, 1915:378; Mocquard, 1909:47; Boettger, 1913:373; Werner, 1925:112; Guibé, 1958:236; Brygoo, 1983: 42, 55, 1987:23; UICN, PNUE, and WWF, 1990: 224; Glaw and Vences, 1992:264, 1994:347.

Geodipsas heimi Angel, 1936:127–128 (type locality, "au long de la rivière Sahandrato, en amont de Tsianovoha" [along the Sahandrato River, upstream from Tsianovoha]). Angel (1936:125) described Tsianovoha as being "SSW of Fort Carnot and of the Ikongo Massif (alt. 600 m)" (= Tsianivoho; 21°57′S, 47°21′E; Fig. 9). Holotype, Muséum National d'Histoire Naturelle, Paris (MNHN) 1936.19, collected by Roger Heim in 1934 or 1935. Guibé, 1958:236; Brygoo, 1983:42, 55, 1987:23; UICN, PNUE, and WWF, 1990:222; Glaw and Vences, 1992:264, 1994:347; Raxworthy and Nussbaum, 1994:68. **New synonymy.**

Holotype (Figs. 7, 8). An adult male in good condition whose mensural and meristic characters are reported in Table 2.

Distribution (Fig. 9). Known from few specimens from the following localities on the eastern escarpment (*Specimens Examined*): the vicinity of the RNP and the nearby locality, Tsianovoho (type locality of *heimi*), Andrangoloaka (type locality of *boulengeri*), "Pays Zafimaniry" (east of Ambositra), and from Perinet (= Andasibe; 18°56′S, 48°25′E; C. A. Domergue, *in litt.*). The recorded elevational range is 600 m (Tsianovoho) to approximately 1,400 m (Andrangoloaka; see Cadle, 1996: fn. 6).

Geodipsas "heimi," here considered a synonym of *G. boulengeri,* has been reported from the vicinity of Montagne d'Ambre (Raxworthy and Nussbaum, 1994; Glaw and Vences, 1994), but all specimens referred to *Geodipsas "heimi"* that I have seen from that area (*Key to species* and *Specimens Examined*: *Geodipsas* species inquirenda) are a distinct species that will be dealt with in a separate treatment. I do not include variation in these northern Madagascar specimens of *"heimi"* in my treatment of *boulengeri,* which I consider to be restricted, as far as presently known, to the eastern escarpment. However, given the few specimens that have appeared since its description more than a century ago, it would hardly be surprising that new specimens could significantly increase the known range of *boulengeri.*

Etymology. The species epithet is a patronym for George A. Boulenger.

Diagnosis. The light (orangish to yellowish in life), curved, postmandibular spots, light spots on the upper and lower labials and gular region, and dusky gular region with irregular light areas, are diagnostic features of *Geodipsas boulengeri* (Fig. 8); the RNP specimen had a brilliant orange venter in life but whether or not this is typical is unknown. The species is essentially indistinguishable from *G. zeny* in scutellational features, but aspects of coloration distinguish the two (see *Diagnosis* in the previous description of *zeny*). *Geodipsas boulengeri* has, in comparison with *G. infralineata* and *G. laphystia* (combined ranges for characters given), fewer ventrals (131–137 vs. >170) and subcaudals (24–36 vs. >50), a shorter tail that is not prehensile (12–16% of total length vs. 17–26% and prehensile), and a different coloration (see species accounts). In comparison to *G. vinckei, boulengeri* has fewer ventrals (131–137 vs. 161) and a different color pattern. *Geodipsas boulengeri* differs from specimens referred to *Geodipsas* species inquirenda from the vi-

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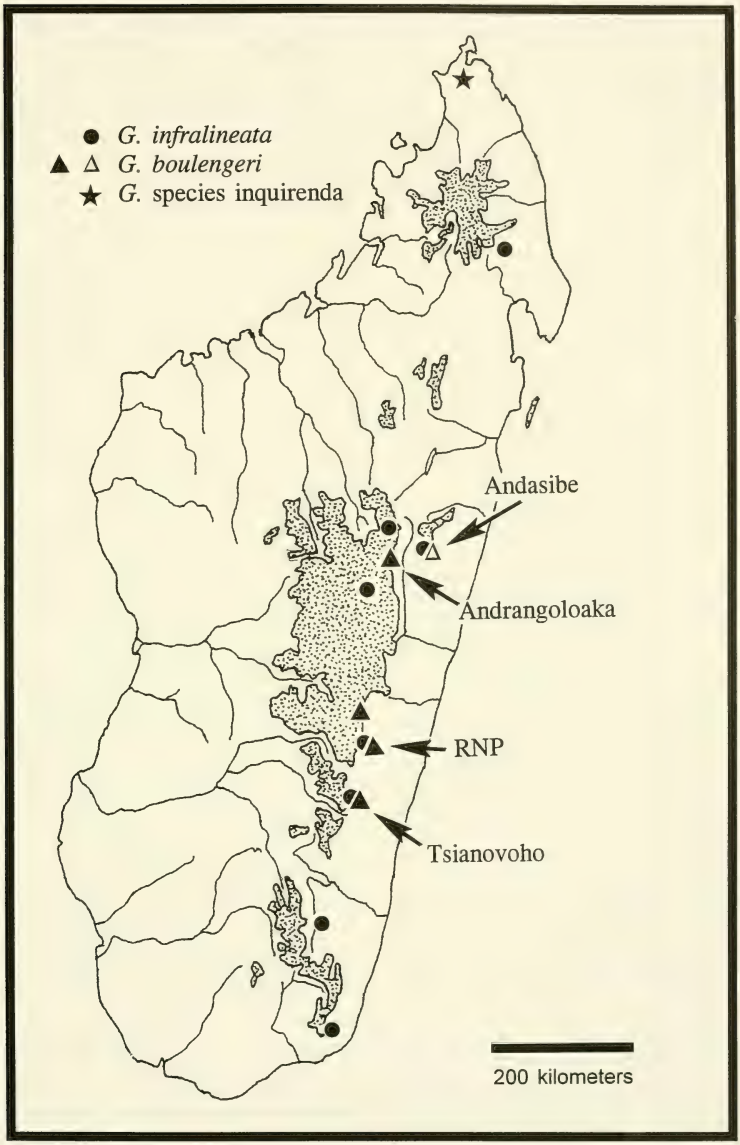
Figure 9. Distributions of species of *Geodipsas* (*boulengeri, infralineata,* and *Geodipsas* species inquirenda) discussed in the text. Type localities are as follows: Andasibe (= Perinet), *Geodipsas vinckei* Domergue (known only from the holotype); Andrangoloaka, *Geodipsas boulengeri* (Peracca); Tsianovoho, *Geodipsas heimi* Angel. All plotted localities based on specimens examined, except for the open triangle for *boulengeri* (see *Distribution*). *Geodipsas infralineata* is reported from many additional localities in the literature (e. g., Glaw and Vences, 1994), but because of its previous confusion with *G. laphystia* these localties are not plotted; it has been reported as far north as the vicinity of Montagne d'Ambre (star). Shaded area is above 1,000 m.


● *G. infralineata*
▲ △ *G. boulengeri*
★ *G.* species inquirenda
Andasibe
Andrangoloaka
RNP
Tsianovoho
200 kilometers

cinity of Montagne d'Ambre (here considered a distinct species) in averaging about 13 fewer ventrals and in subtle aspects of coloration (see *Key to Species*).

Description. Measurements, proportions, and scutellation are summarized in Table 1. Peracca's (1892) description of the type is detailed and excellent.[5] Largest male (MNHN 1936.19, holotype of *G. heimi*), 353 mm total length, 55 mm tail length. No adult female available. Tail length 12–16% of total length. Body slightly higher than wide; ventrolateral edge of body angulate. Head slightly wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior scale-row reduction usually by loss of row 4 at the level of ventrals 83–108 (N = 6 sides; appearing as fusion of 3 + 4 on one side). Ventrals 131–137 (preceded by 2 preventrals). Anal plate single. Subcaudals 24–36.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials 8–9 (bilateral asymmetry) in 3 adults (range 6–9 in a series of hatchlings, most of which have unusual asymmetries in infralabial counts, e.g., 7–6 to 9–9); the first pair in contact behind the mental, 1–4 touching an anterior genial, 4–5 touching a posterior genial. Anterior genials shorter than, or approximately equal to, posterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 15–18 + 2 ($\bar{x}$ = 16.3 ± 0.95; modes 17 and 16; N = 10). Diastema approximately 1.5× the width of the posteriormost solid teeth. The fangs are about 1.5× as large as the posteriormost maxillary teeth and are deeply grooved for most of their length. There appears to be a narrow cutting edge on the distal end of the posterior surface. The tips of the fangs are slightly compressed. The ultimate fang is offset laterad from the tooth row.

Hemipenis (See Fig. 16 and Detailed Description, Later). Single (nonbilobed), noncapitate, and acalyculate; proximally nude, with a spinose midsection. Distal region spinulate, more or less sharply set off from the midsection by its distinct ornamentation. Sulcus spermaticus centrolineal, terminally forked, but the forked portion is so short that the distal tip of the sulcus simply appears to have a broad expansion.

Coloration in Life (MCZ 181163). Dorsum reddish brown with somewhat obscure orangish flecks from the nape to the tail, one series laterally along the flanks and another parallel series paravertebrally. Paired bright orange spots on lateral surface of neck with a thin brown border. Iris reddish brown to reddish orange. Top and sides of head reddish brown. Upper and lower labials reddish brown, each with pale yellow spot (more vivid on upper labials). Throat orangish brown (orange ground color with brown suffusion). Entire ventral surfaces (body and tail) bright orange. Lateral surface of ventrals edged with reddish brown (probably resulting from encroachment of brown dorsal pigment laterally onto orange ventral scutes).

Coloration in Preservative. The holotype (MZUT 1874) and MCZ 181163 are similar in coloration; the type of *Geodipsas heimi* is considerably darkened. A series of six hatchlings (MNHN 1986.1373–78) appear to be naturally darker than the adult specimens and probably were in life; they are described separately below. Overall dorsal coloration of adults is medium brown with a fine suffusion of darker brown that tends to highlight the edges of the dorsal scales. Under high magnification, individual dorsal scales are marbled with brown and tan flecks and reticula-

[5] The subcaudal count of the type (Table 2) is correct and is identical to a hand-written correction of the count in the MCZ library and other copies of the original description; these hand corrections, very likely made by Peracca or at his direction, are discussed by Cadle (1996:*Remarks* under *Liopholidophis dolicocercus*).

tions. The labial and postmandibular spots and the light dorsal flecks are off-white. Gular region dusky with light spots. Venter off-white, with encroachment of brown dorsal pigment laterally. MNHN 1936.19 has a line of dark speckling (not discrete spots) down the middle of the venter and subcaudals from the neck to the tail tip; MZUT 1874 and MCZ 181163 have no such markings.

A series of hatchlings (MNHN 1986. 1373–78) shows a series of narrow, interrupted, light crossbands formed by alignment of the light dorsal flecks; these are offset on the lower flanks. The bands are about 2 scale rows apart, and formed by light flecking on rows 4 and 7–8 on either side, occasionally encompassing adjacent rows as well. These crossbands are vivid in five of the hatchings but absent in the sixth (MNHN 1986.1374). The dorsal ground color of the hatchlings is much darker brown than that of adult *boulengeri*.

In the holotype (MZUT 1874; Fig. 7), the dorsal light flecks are more apparent than in the preserved (adult) RNP specimen, and their distribution is similar to that in the hatchlings just described. The holotype may have had discrete, but interrupted, crossbands in life similar to that of the hatchlings.

Natural History. MCZ 181163 was collected 24 October 1990 while active at 1435 hours on a trail within primary montane rainforest (but selectively logged >50 years ago). Angel (1936) stated that the type of *Geodipsas heimi* was collected in "a marshy grassland along [a river]," but he did not give the time of day. No special defensive behaviors (biting, gland secretions, etc.) were observed in MCZ 181163, and Angel (1936) reported that the type of *G. heimi* "never [sought] to react or to bite" while being handled.

Geodipsas boulengeri is an infrequently encountered snake in its known range. Only a single specimen was obtained during the 1990–95 Ranomafana survey, and other localities, except for the series of hatchlings from one locality, also are represented by single specimens.

Although there are few reported observations of *Geodipsas boulengeri*, several characteristics of body form suggest cryptozoic habits (see Cadle and Greene, 1993, for discussion). These include a short, blunt head little distinct from the neck, a relatively short tail (Table 1), and round body. Certainly, no characteristics of the body form of *G. boulengeri* suggest arboreal proclivities in this species as has been observed in *laphystia, zeny,* and *infralineata.* The rarity with which this species seems to be encountered may, in part, reflect secretive habits.

Geodipsas infralineata (Günther)

Figures 10–12; Table 1

Tachymenis infralineatus Günther, 1882:265 (type locality, "Eastern Betsileo"). *Inferred* holotype, BMNH 95.10.29.61, an adult female collected by Reverend William Deans Cowan. This specimen is *not* the specimen labeled as the type during the period immediately following World War II, and it bears this number probably as a result of a specimen mixup that occurred between 1896 and the 1940s (see comments below). The type is unquestionably the specimen illustrated by Boulenger (1896:pl. III, fig. 1).

Geodipsas infralineata (Günther): Boulenger, 1896: 32, 1915:378; Boettger, 1898:89; 1913:271, 373; Mocquard, 1909:47; Werner, 1925:112; Mertens, 1933:273; Angel, 1936:127; Guibé, 1958:235; Brygoo, 1983:42, 55, 1987:23; Nicoll and Langrand, 1989:135; UICN, PNUE, and WWF, 1990:222; Glaw and Vences, 1992:264, 1994:346; Raxworthy and Nussbaum, 1994:68.

The Holotype of Geodipsas infralineata *(Günther).* During examination of the holotype and other specimens of *Geodipsas infralineata* in The Natural History Museum (London) (BMNH), I discovered an apparent mislabeling and misnumbering of the type specimen. I was, however, able to infer the correct type based on comparison of BMNH specimens with details given for the type by Günther (1882:265–266) and Boulenger (1896:32). Here I clarify this confusion over the type.

The specimen presently (but, I believe, erroneously) *labeled* "holotype" of *Geodip-*

sas infralineata is an adult female, BMNH 1946.1.7.20 (old number 82.5.8.1).[6] My measurements and ventral/ subcaudal counts for this specimen are as follows: total length 679 mm, tail length 122 mm, ventrals 173, subcaudals 53. Günther's (1882) description gave the following for the holotype (and then the only specimen available): total length 31 in. (= 787 mm), tail length 6 in. (= 152 mm), ventrals 186, subcaudals 62. Boulenger (1896) reported ventral and subcaudal counts for the type as 187 and 62, respectively. Clearly, BMNH 1946.1.7.20 conforms poorly with these details.

However, my scale counts and measurements for another adult female, BMNH 95.10.29.61, conform well with the details reported by Günther and Boulenger for the type of *Geodipsas infralineata*: total length 761 mm, tail length 151 mm, ventrals 183.5 + 2 preventrals (= 185.5), subcaudals 61. I conclude that an apparent switch of specimens occurred sometime between 1896, when Boulenger's catalog was published, and the early 1940s, when types were evacuated to caves for safekeeping. Because the specimens would have been untagged during the intervening period, the possibility of a mixup was greatly increased. When types were recataloged in 1946, the incorrect specimen was reinstalled in the type collection and subsequently tagged with the incorrect catalog number.

Additional circumstantial evidence that BMNH 95.10.29.61 is the type of *infralineata* is that, of the two specimens in question, this is clearly the one illustrated by Boulenger (1896:pl. III, fig. 1), as indicated by two unusual features: (1) a peculiar circular marking on the nape that has a pair of asymmetrical posterior "spurs" and (2) a distinct postocular stripe on the left side (the one illustrated by Boulenger) that is connected to the dark markings on the dorsum of the neck. Neither of these features is evident in BMNH 1946.1.7.20, which has different dark neck and head markings. Boulenger seems to have used type material for illustrations in his catalogs when such specimens were available. Thus, the conjunction of the measurements, scale counts, and illustration virtually prove that BMNH 95.10. 29.61 is the type of *Geodipsas infralineata* (Günther).

The scale counts for the other specimen, BMNH 1946.1.7.20, correspond to those Boulenger (1896:32) gave for the only other specimen of *Geodipsas infralineata* in the British Museum collection at that time: 172 ventrals and 55 subcaudals. Other details given by Günther and Boulenger on the holotype do not permit unambiguous association with either BMNH 1946.1.7.20 or 95.10.29.61. Hence, I infer that the correct original identity of BMNH 1946.1.7.20 is the specimen with similar ventral and subcaudal counts reported by Boulenger (1896), and its correct catalog number should be 95.10.29.61. The specimen now residing under number 95.10.29.61 is the holotype of *Geodipsas infralineata* (Günther) and would have originally born the old number 82.5.81.

BMNH 95.10.26.61 is an adult female (measurements and basic scale counts already given), rather soft, and in fair condition. It is now faded to a dirty yellowish white, although narrow diagonal dark dorsal lines, a posterior middorsal dark longitudinal stripe, and a dark midventral stripe are still evident. Narrow, dark dorsal diagonals are evidenced by dark brown edges to the dorsal scales, which are otherwise beige; successive diagonals are separated generally by two scale rows (typical for other specimens I have examined) and are evident from the head to the vent (more distinct posteriorly). The skin has been peeled back from the cranium and mandible, and the posterior abdominal region and proximoventral tail regions have

[6] Through consultation with Drs. E. N. Arnold and C. J. McCarthy, this specimen will be retained in the type collection with its current labeling as the holotype, but the inferred correct holotype (see later) will also be placed in the type collection.

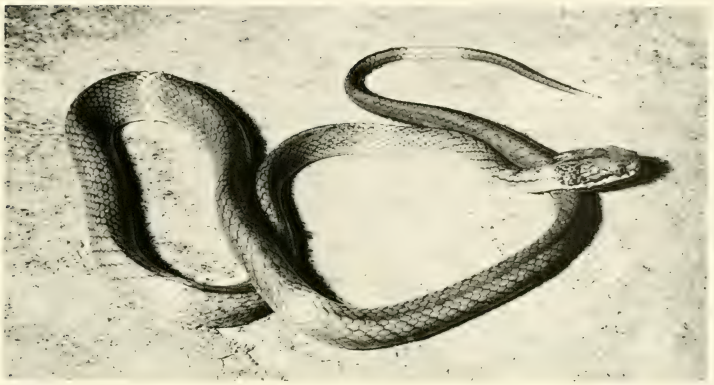


Figure 10. *Geodipsas infralineata* (MCZ 181153; total length 597 mm). Specimen from the RNP. The fine dark diagonals on the flanks are characteristic of most specimens of this species. The dark vertebral line and dark nape blotches are present in many specimens, but not universally.

been slit. The details of scutellation and pattern reported by Günther (1882) are essentially correct (differences as already noted above), although the pattern is now greatly faded and Günther did not mention the fine diagonal dark dorsal lines visible in the specimen; the last feature is here considered a diagnostic difference between *infralineata* and *laphystia* (see *Diagnosis* in the description of *laphystia*).

Distribution (Fig. 9; Specimens Examined). Geodipsas infralineata is widely distributed in the eastern rainforests and adjacent plateau, but its precise range will not be known until older records are reexamined to verify whether *infralineata* or *laphystia* was their basis. I have seen specimens unquestionably referable to *infralineata* from "mountains north of Fort Dauphin" (= Tolagnaro; 25°02′S, 47°00′E; MNHN 1986.1390) in the south to approximately latitude 18°S in the north (e.g., MNHN 1986.1392, 1978.91–92, 1978.94); all of these compare well with the type and to the diagnosis given later. One specimen from Marojezy (14°26′S) has an unusual pattern but is referred to *G. infralineata* for lack of a reasonable alternative (see *Coloration in Preservative*). At least one specimen I examined confirms a locality on the high plateau (Manjakatompo, 19°20′S 47°26′E; MNHN 1957.731; another specimen is questionably from the plateau: MNHN 1986.1392; see *Specimens Examined*). Most specimens seem to be from upland rainforests, although the recorded elevational range is broad (300–2,000 m).

Glaw and Vences (1994) reported several localities from northern Madagascar from the vicinity of Maroantsetra to Montagne d'Ambre (15°30′ to 12°30′S), and Raxworthy and Nussbaum (1994) listed *G. infralineata* for Montagne d'Ambre. Glaw and Vences, at least, included *G. laphystia* within their concept of *infralineata* (e.g., their figs. 514–515), so these records should be reexamined to confirm their identity.

Etymology. The species epithet refers to a narrow dark midventral line that is present in many specimens, including the holotype (Boulenger, 1896:pl. III, fig. 1b; Fig. 12).

Diagnosis. Geodipsas infralineata is larger than other species of *Geodipsas* (to >750 mm total length in males, >900 mm in females). It has a relatively high number

of ventrals (172–199) and subcaudals (53–77), a distinctly compressed body, and a prehensile tail. The typical pattern for most specimens (Fig. 10; see sections on coloration, later) is a series of fine dark diagonal lines on the flanks superimposed on a yellowish, grayish, or brownish ground color; the diagonals are formed by darkened edges to scale rows, and successive diagonals are usually separated by 2 scale rows.

Geodipsas infralineata differs from *vinckei* in averaging more subcaudals ($\bar{x}$ > 60 in both sexes, vs. 45) and in lacking a light collar on the nape (present in *vinckei*). Domergue (1988) reported the body of *G. vinckei* as "cylindrical," but the type (only known specimen) is rather dessicated and has the appearance of having a somewhat compressed body and, thus, may be similar to *infralineata* in this respect. *Geodipsas infralineata* is easily separated from *G. zeny* and *G. boulengeri* on the basis of both color pattern and scale counts (see Table 1 and species accounts for the latter species for details). *Geodipsas infralineata* is most easily confused with *G. laphystia,* which differs from *infralineata* primarily in having a series of longitudinal lines (rather than diagonals) on the flanks and in other scutellational and hemipenial characters; see the description and diagnosis of *laphystia* for details.

Description. Measurements, proportions, and scutellation are summarized in Table 1. Largest specimen a female (MCZ 181142), 933 mm total length, 168 mm tail length; largest male (MNHN 1978.90) 783 mm total length, 148 mm tail length. Tail length 17–23% of total length in males, 17–21% in females. Body strongly compressed, higher than wide, and with a strongly angulate ventrolateral edge; neck and anterior body somewhat attenuate. Head wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior scale-row reduction usually by fusion of rows 3 + 4 at the level of ventrals 114–129 (N = 16 sides); rarely fusion of rows 4 + 5 (both sides of 1 specimen). Ventrals 172–193 in males, 173–199 in females, usually preceded by 2 preventrals. Anal plate single. Subcaudals 53–77 in males, 53–68 in females.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials 9–9 (N = 13), 9–10 (4); or 8–9, 8–10, or 10–10 (1 each); the first pair in contact behind the mental, 1–4 touching an anterior genial, 4–5 touching a posterior genial. Anterior genials shorter than posterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 15–18 + 2 (N = 15). Modal number of prediastemal teeth 16 (N = 6), followed by 15 and 18 (4 each) and 17 (1). Diastema very short, equal to or less than the width of posterior solid maxillary teeth. The fangs are deeply grooved, about twice as large as the posteriormost solid teeth, have a narrow knifelike posterior edge distally, and are slightly compressed at the tips. The ultimate fang is offset laterad from the tooth row.

Hemipenis (See Fig. 17). Single (nonbilobed), noncapitate, and acalyculate; proximally more or less nude, having a spinose midsection, and distal spinulate region that forms a more or less distinct head. Sulcus spermaticus centrolineal, forked distally for approximately 20% of its length, and not reaching the apex of the everted organ. The asulcate side bears 2 rows of large, hooked spines, the rows slightly diverging distally and each having 4 spines.

Coloration in Life (See Glaw and Vences, 1994:pl. 336). Geodipsas infralineata is highly polymorphic in coloration, even within the limits of the RNP. The color tones do not appear to be correlated with size or sex, although smaller individuals tend to be of lighter shades than larger ones having similar tones. Although I

have seen live specimens only from the RNP and from the vicinity of Midongy du Sud (MCZ specimens listed in *Specimens Examined*), coloration of specimens from the latter locality (N = 2) was within the range of colors seen in the RNP (N = 7). My description of colors in life are based on these specimens.

The general dorsal ground color is pale yellow or deep yellow, medium brown, grayish brown, or dark grayish brown. Most specimens have some indication of narrow dark brown or blackish diagonal lines on the flanks from the neck to the tail base. These diagonals extend from the vertebral scale row posteriorly, following a suture line between 2 dorsal rows, down to row 3 or 4 from the ventral plates. The bilateral arrangement of the diagonals is symmetrical, so that when viewed middorsally pairs of diagonals on either side form narrow chevrons. Successive diagonals are separated by 2 dorsal rows, although occasionally another diagonal may be intercalated or an extra scale row may be "skipped."

Many specimens have a middorsal series of dark dashes or dots that may fuse posteriorly to form a dark vertebral line. Most specimens have some indication of a dark postocular bar or streak extending from the posteroventral edge of the eye, across the upper edge of the posterior supralabials, and ending at the jaw angle. A pair of dark nape spots, as well as a dark streak along the interparietal suture, may be prominent or indistinct (Fig. 10). Iris grayish brown to yellowish brown.

Ventral ground color whitish to yellow, occasionally with an orange suffusion, and with varying amounts of dark (brownish to grayish) flecking, spotting, or suffusion. The dark ventral spots or flecks often concentrate toward the midventral line posteriorly, forming a line of spots or an unbroken midventral line (Fig. 11). After a brief interruption at the vent, the line continues to the tail tip; although often discontinuous anterior to the vent, the midventral line is usually more or less continuous on the tail, although of variable width. In individuals with a brownish to grayish dorsal ground color, the dorsal color encroaches laterally onto the ventral scales.

The lack of correlation between dorsal coloration and either size or sex is emphasized by comparison of several specimens with contrasting colors: Of the 2 largest specimens, both females, one (MCZ 181147; SVL 765 mm) has a dark grayish brown ground color, whereas the other (MCZ 181160; SVL 713 mm) is bright yellow, somewhat darkened by brownish suffusion. A much smaller male (MCZ 181153; SVL 460 mm) is similar in coloration to MCZ 181147, whereas another male of similar size (MCZ 181157; SVL 491 mm) had an overall yellowish ground color.

The following color notes for particular specimens give additional details and characterize the color variation further.

MCZ 181147 (female, SVL 765 mm): Dorsum gray-brown with heavy black speckling, tending to form ill-defined vertebral stripe along most of body. From the vertebral line, narrow blackish diagonals extend posteriorly along dorsal scale sutures, reaching approximately the third dorsal row; successive diagonals separated by 2 scale rows. Ground color of top of head similar to dorsum, with paired black nape patches (not very distinct). Black postorbital stripe to corner of mouth. Venter dull white with black squarish spots concentrated midventrally and forming a line. Chin, throat, and anterior venter whitish without markings (Fig. 11).

MCZ 181149 (female, SVL 661 mm): Dorsum brown, but under magnification each scale is minutely mottled with brown/grayish brown. Interrupted vertebral black stripe beginning about midbody and continuing to tail tip; narrow dorsal diagonals as in MCZ 181147. Scattered black flecks on anterior ½ of dorsum. Iris reddish brown. Top of head brown flecked with black. A pair of brown nape blotches slightly darker than ground color. Upper

labials brownish cream flecked with black. Indistinct black postorbital bar to corner of mouth. Lower labials and throat creamy white flecked with dark brown. Venter anteriorly dull cream, with yellowish wash posteriorly (last ⅔ of body), heavily speckled with dark brown. Lateral edges of ventrals brown. Posteriorly on body and tail, dark pigment of ventrals concentrated medially, giving impression of irregular midventral stripe. Vague black ventrolateral stripe on tail. Subcaudals creamy with dark brown/blackish midventral stripe.

My other notes on individual specimens describe the dorsal ground colors as rich yellowish to orangish brown (MCZ 181155), tan with yellowish wash (MCZ 181156), or dark grayish brown (MCZ 181153). The ventral ground colors were usually pale yellow, but occasionally dirty white heavily speckled with dark brown/gray (MCZ 181153), or had an orange wash that intensified posteriorly (MCZ 181155).

Coloration in Preservative. Dorsal ground color yellowish, gray, brown, or grayish brown. Many scale borders outlined in black, often forming narrow chevrons, a dark network, a pair of lines on the flanks, or a middorsal line (sometimes a combination of these). A narrow dark postocular stripe extending across top of posterior supralabials and ending at the jaw angle. Ventrals and subcaudals pale yellow or whitish with a median series of punctations or a median line; outer edges of ventrals often with dark markings forming a more or less continuous line at border between ventrals and dorsals.

In addition to considerable variation in coloration in life, *Geodipsas infralineata* also shows much variation in overall dorsal pattern, but I have detected no geographic trends. Some specimens are virtually unicolor dorsally (e.g., Glaw and Vences [1994:pl. 336], MNHN 1986.1391, BMNH 1946.1.7.20) and show no indications of darker markings. In other specimens, the dorsum is virtually unicolor except for a dark brown vertebral stripe from the head to the tail tip (e.g., Henkel and Schmidt [1995:274] and MNHN 1947.7; this last specimen appears to have been sun-bleached and may have lost pattern elements, but the photograph in Henkel and Schmidt is of a live animal). In yet another specimen (MNHN 1978.93), the dark diagonals were manifested only by series of dark flecks, so that the snake appeared spotted and only by close inspection could the details of the diagonals be made out. Although I have referred these unusually patterned snakes to *Geodipsas infralineata*, additional study could demonstrate that other taxa are involved—a possibility that should especially be kept in mind given the previous confusion of *laphystia* with *infralineata*.

Natural History. Because of the confusion of *Geodipsas infralineata* with *G. laphystia*, it is impossible to discern with certainty to which species statements about natural history in previous literature apply. For example, Glaw and Vences' (1994) observation of active specimens of "*infralineata*" at night at the edge of a pool (Andasibe) and during rains (Manjakatompo) appear more typical of *G. laphystia* than of *infralineata*, based on comparison with my observations of habitat and behavioral differences between the two species (see species account for *laphystia*). Glaw and Vences also reported finding two specimens of *infralineata* in a Travellers' Palm (*Ravenala*) and in the trunk of a tree fern (both presumably inactive during the day, although not stated). Angel (1936) reported a specimen of *Geodipsas infralineata* found in a "grassy clearing in islands of degraded forest" at 1,220 m elevation.

All specimens I collected were from primary montane rainforest except MCZ 181157, which came from a relatively high-elevation (1,130 m) forest with a low canopy (6–8 m) and interspersed with grassy meadows; this habitat seems qualitatively similar to the high-elevation habitat reported by Angel (1936) and may be characteristic of some of the "plateau" localities known for *G. infralineata* (see *Distribution*). The following paragraphs ex-

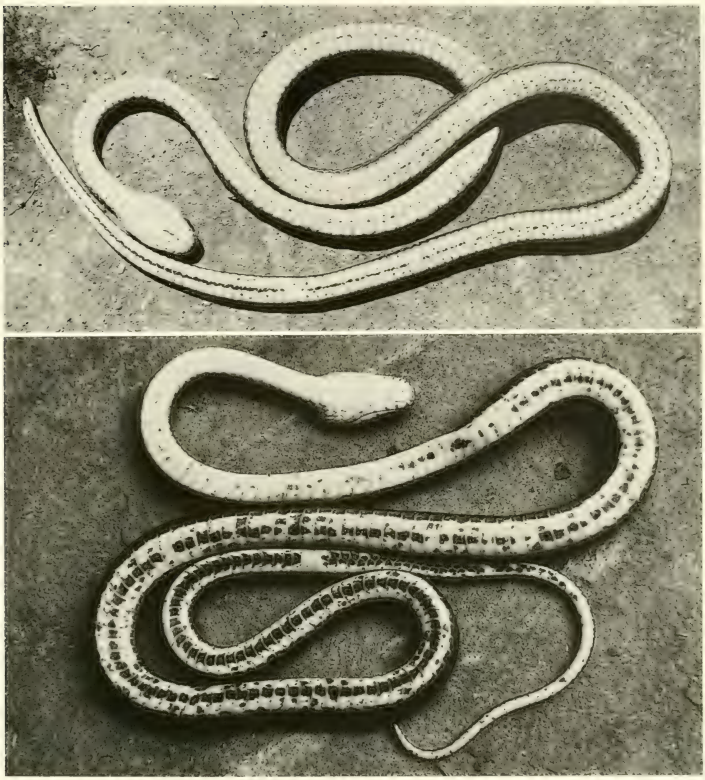


Figure 11. Variation in ventral pattern of *Geodipsas infralineata.* Top, MCZ 181154. Bottom, MCZ 181147. Both specimens from the RNP. Most specimens have some indication of a midventral line at least posteriorly (sometimes much more extensive). Some individuals have much more extensive ventral pigmentation than MCZ 181147.

tracted from my field notes discuss specific circumstances in which this species was encountered; with the exception of the first instance described, all observations were nocturnal.

The only specimen of *Geodipsas infralineata* found during the day (MCZ 181147) was collected by ornithologist Steve Zack. The snake was encountered during morning (daylight) hours within 1 m of a nest of *Tylas edwardii* (Aves: Vangidae) placed about 4 m up in a small tree; the nest contained young. The snake, a large female (total length 933 mm), was being mobbed by the adult birds using calls and spread wing postures. A color slide taken by Zack of the head and anterior portion of the snake in ventral perspective shows the anterior 15 cm of the body dorsoventrally flattened (Zack, *in litt.*, reported that the anterior 20 cm of the body was flattened, not all of which was captured in the photograph). The snake was immobile during the period of observation. Such a display was not seen

in other individuals of *G. infralineata* that I observed.

Dorsoventral flattening of the neck is a very unusual defensive display for arboreal snakes. For example, Greene (1979) surveyed 77 genera (129 species) of snakes for three defensive displays (tail displays, lateral neck compression, dorsoventral neck flattening) and found no arboreal snakes using neck flattening (neck compression is a common display in arboreal snakes). He later (Greene, 1988) reported three species of arboreal elapids (*Dendroaspis* and *Pseudohaje*) that use neck flattening. Nevertheless, neck flattening as seen in *Geodipsas infralineata* seems to be a very uncommon display in arboreal snakes. (Greene [1988] also listed this behavior for the arboreal African colubrid, *Dispholidus,* but that seems to be based on a qualitatively different behavioral repertoire in which the neck is actually inflated in a horizontal plane.)

Other circumstances of capture of *Geodipsas infralineata* were as follows (all nocturnal observations). MCZ 181157 was loosely coiled about 2 m up in a small tree in high-elevation forest interspersed with meadows. MCZ 181149 was collected 6–7 m above ground in montane rainforest away from streams, and MCZ 181153 was in montane rainforest 4 m aboveground on a vertical climbing bamboo stem that was suspended from high in the overlying canopy. The only *infralineata* on the "ground" was MCZ 181160, a large female, which was crawling (not swimming) slowly across a small, flowing forest stream with its body submerged onto the stream bottom (20 cm deep) and its head projecting above the surface.

MCZ 181149 was observed on two occasions 30–45 min apart in more or less the same position, 6–7 m aboveground in a tree; although moving slowly in each case, the snake clearly had no strong directional orientation. Several other snakes on low vegetation exhibited the same sort of nondirectional movements, and for many specimens it seemed likely that they could have been found in more or less the same positions over extended periods in a single night.

All observations suggest that *Geodipsas infralineata* is a primarily arboreal snake. Even in the absence of direct observations, however, this could be inferred from aspects of body form (see Cadle and Greene, 1993:table 25.1; Guyer and Donnelly, 1990). The body is relatively attenuate and compressed, with a narrow "neck" region and relatively broad head. The ventrolateral edge of the body is angulate and the tail is relatively long and strongly prehensile. All of these are characteristic of arboreal colubrids and suggest strong arboreal proclivities for *Geodipsas infralineata. Geodipsas infralineata* also has a bright yellow eyeshine, which is characteristic of some nocturnal snakes.

Only two food records were obtained for *Geodipsas infralineata,* both from the same specimen. MCZ 181149 (SVL 661 mm) contained an unidentified frog in its stomach and four tiny mammal claws and a few mammal hairs in its intestine (along with fragments of arthropod chitin, which may have been secondarily ingested). This specimen is one of the larger *infralineata* collected. I suspect that frogs (and possibly their eggs, as in *G. laphystia*) are the dietary staple of smaller individuals of *G. infralineata,* whereas larger adults probably consume frogs as well as mammals. Such ontogenetic broadening of the diet is known for many species of colubrids that consume ectothermic vertebrates at small body sizes (e.g., Greene, 1989). The identity of the mammal in MCZ 181149 can only be guessed but was likely one of the arboreal rodents known from Talatakely in the Ranomafana National Park (*Eliurus tanala* and *Brachytarsomys albicauda* [Muridae: Nesomyinae]). Based on size alone the claws were probably of a juvenile or nestling. Henkel and Schmidt (1995: 274) stated that *Geodipsas infralineata* (probably including *laphystia*) ate frogs but that "lizards and small rodents were

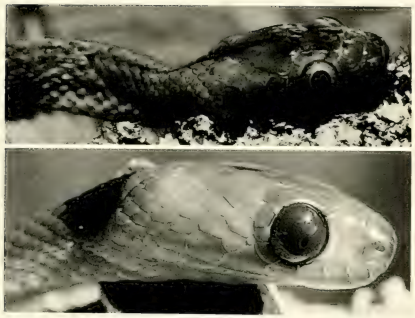


Figure 12. Prolate pupils in *Geodipsas laphystia* (top, MCZ 181387) and *Lycodryas* [*Stenophis*] *arctifasciatus* (bottom, MCZ 181431). In *Geodipsas* the pupil is a large, broad oval, whereas in *Lycodryas arctifasciatus* (but not *L. betsileanus*; see text) the pupil contracts to a small ellipse. These are qualitatively different from narrowly elliptical (slitlike) pupils (see Fig. 13).

Figure 13. Elliptical pupil of *Madagascarophis* sp. (MCZ 181433). Note the strongly angulate dorsal and ventral borders in this slitlike pupil.

not scorned"; these observations were probably based on captive feeding records.

Geodipsas infralineata is presumably oviparous, as apparently are two of the African species of *Geodipsas* (Rasmussen et al., 1995) and most other Malagasy snakes for which that information is available (Glaw and Vences, 1994; Cadle, 1996). Henkel and Schmidt (1995) stated, without documentation, that *G. infralineata* lays eggs. Three adult females of *infralineata* (SVLs 661–765 mm; MCZ 181147, 181149, 181160) were collected, but only MCZ 181160, collected 13 January 1993, showed evidence of vitellogenesis (follicles <5 mm diameter). The other two females were collected from 25 October to 4 November 1990 and had nonyolking follicles.

No *Geodipsas infralineata* attempted to bite, although individuals struggled to escape upon capture. Most specimens emitted a foul-smelling secretion from the scent glands in the base of the tail.

Remarks. Two Malagasy names are used for *Geodipsas infralineata* in the Ranomafana region. *Mandochala* (män-dü'-chälä) was used near the village of Sahavandrona (western edge of the RNP) and does not seem widespread. More commonly encountered was the name *lapata* (lä-pät'-ä). This name is also used for the other nocturnal arboreal colubrids known from the area, *G. laphystia* and *Lycodryas betsileanus*, and seems to be a general term for nocturnal arboreal colubrids (*G. infralineata* and *G. laphystia* are not distinguished by locals).

DISCUSSION

Pupil Shape in Geodipsas

My observations of pupil shape in Malagasy *Geodipsas* differ from those given in the literature and here I clarify these discrepancies. Boulenger (1896), Guibé (1958), and Glaw and Vences (1994) have described pupil shape of Malagasy *Geodipsas* as "round" or "circular" (in fact, this character is part of the definition of the genus given by Boulenger). However, most Malagasy specimens I examined are better characterized as "subcircular" in the sense of Myers (1984). In preserved specimens, the pupil shape varies from more or less round to prolate (narrowed laterally); the latter seems to be the usual condition. In daylight, the pupil contracts to a broad ellipse (Fig. 12; see also Glaw and Vences, 1994:pl. 336, fig. 515), but not to the extent usually connoted by the descriptor "elliptical," which refers to a qualitatively different pupil form in its fully contracted state. Rather than a broad prolate ellipse, truly elliptical pupils (e.g., in *Madagascarophis*, Fig. 13; see also Glaw and Vences, 1994:fig. 497) form a narrow vertical slit. I

concur with Myers (1984) that the distinction between subcircular and elliptical pupils is a useful one because of its potential systematic or functional significance.

The prolate pupil of Malagasy species of *Geodipsas* contrasts with that of the three African species, which seems to be truly round based on examination of preserved specimens of all three species in the MCZ (one of 16 *G. vauerocegae* examined appeared to have a prolate pupil). This is one character in which the African species differ from the Malagasy species.

Similar confusion in the literature concerning pupil shape exists for other Malagasy colubrid genera. For example, Guibé (1958:243) described the pupil of *Alluaudina,* which is possibly closely related to Malagasy *Geodipsas* (see later), as "vertically elliptical," although none of his figures, nor those of Domergue (1984) for *A. bellyi* or *A. mocquardi,* show such a shape. Domergue (1984) expressed similar confusion. Glaw and Vences (1994:330) commented "Pupil is circular [in *Alluaudina*], but has also been described as vertical elliptic." The confusion seems to stem from failure to distinguish subcircular and more strongly elliptical forms. Mocquard's (1894:9) original description was probably correct when he stated that *Alluaudina* has a "pupil a little elongate vertically," that is, subcircular in the sense of Myers (1984) (see also Domergue, 1984:539). A subcircular pupil shape is one of several characters shared by *Geodipsas* and *Alluaudina* that might suggest a relationship between these two genera (see later). Domergue (1984:539) remarked that one specimen of *Alluaudina bellyi* had a small pupil, weakly elongated vertically, and "could be compared to that of certain *Lycodryas*" (*Stenophis sensu* Domergue [1994] and Glaw and Vences [1994]). My study of *Lycodryas sensu lato* in the MCZ (including *betsileanus, arctifasciatus,* and *granuliceps*) suggests that these species also have prolate pupils. The pupil of *L. betsileanus* appears similar to that of *Geodipsas* (i.e., a broad prolate ellipse when contracted), whereas the pupil of the other two *Lycodryas* contracts to a much smaller prolate opening (Fig. 12).

Osteology of *Geodipsas laphystia* (Hypapophyses and Skull)

Because of the scarcity of osteological material of species of *Geodipsas* in collections, I do not attempt comprehensive comparisons here. I record salient features of the skull and hypapophyses of *Geodipsas laphystia,* the only species whose osteology I have studied. I examined two skeletons of *Geodipsas laphystia* (MCZ 181164–65; both adult females ≥578 mm total length; the skull of MCZ 181164 is largely disarticulated). In the following account, when specific observations are reported for each specimen separately, the observations are given first for MCZ 181164, then 181165.

Vertebral Hypapophyses. Well-developed hypapophyses are present on all trunk vertebrae of *Geodipsas.*[7] In *G. laphystia,* there are few substantive qualitative differences between the anterior and posterior hypapophyses aside from somewhat greater robustness of the posterior ones. Thus, this account refers specifically to the posterior hypapophyses. The overall form of the hypapophyses is sigmoidal: after a short projection posteroventrally from the centrum, the hypapophysis turns posteriorly so that the distal tip is directed posteriad. The distal tip is slightly bifid (not observed on anterior hypapophyses) and extends well beyond the condyle edge. A prominent anterior keel extends forward from the base of the hypapophysis to the rim of the cotyle. The ventral edges of the hypapophyses are a slightly flattened blade.

General Features of the Skull of Geodipsas laphystia. The skull of *Geodipsas laphystia* is lightly built and of ordinary

[7] Other than superficial examination of *G. zeny, G. boulengeri,* and *G. infralineata* to verify the presence of posterior hypapophyses, I did not examine the morphology of these species in detail.

colubrid proportions (e.g., not showing unusual proportions of features such as the orbits or snout that are sometimes observed in burrowing or arboreal snakes).

Tooth Counts, Fangs, and Tooth-Bearing Bones. Maxillary teeth (left and right counts separated by a solidus for each specimen): 19/19, 20/19 prediastemal teeth, followed in each case by two enlarged grooved fangs. The fangs are approximately 1.5× the size of the posterior solid tooth; they bear a prominent groove on the anterior face and narrow cutting edges on the distal ⅓ of both anterior and posterior faces. Palatine teeth 12/11, 13/12. Pterygoid teeth 21/21, 24/25. Dentary teeth 27/28, 29/28. The maxillary diastema is approximately 1.5× the width of the posteriormost prediastemal tooth in MCZ 181164 and approximately twice the width in 181165. The teeth on all bones are rather long, narrow, and strongly curved. The pterygoids are toothed nearly to the point of lateral flaring.

Skull Roof. The dorsal laminae of the nasals are greatly emarginated anterolaterally and posterolaterally (nasals abut the frontals only narrowly at the midline). The maxillary processes of the premaxilla are long and overlap the anterior ends of the maxillae to approximately the second maxillary tooth. The nasal process of the premaxilla is rectangular and somewhat concave and meets the nasals in a short transverse joint. The two posteromedial processes of the premaxilla are separated by a deep indentation. The postorbital narrowly, but clearly, is separated from the frontal by a short parietal flange. The parietal table is flat, bordered posterolaterally with prominent ridges for muscle attachment that converge posteriorly; posterior angle of the parietal broad, obtuse.

Orbital Region. The frontals extend ventrally to slightly overlap the dorsal margin of the trabecular grooves, but at no point are the grooves completely obscured from lateral aspect. Correspondingly, there is a short frontal step on the sphenoid. The frontals and parietal are not emarginated around the orbital foramen, which is rather small; thus, only a short gap separates the ventral borders of the frontals and the anteroventral parietal edge at the orbital foramen.

Basicranial Region. The parasphenoid portion of the sphenoid is roughly triangular, with long, gradually converging sides stemming from the basisphenoid (i.e., no narrow cultriform process with relatively straight sides; see Cadle, 1996:448, 450). Ventrally, the parasphenoid bears a deep median groove extending the entire length of the parasphenoid. Anteriorly, the parasphenoid ends in a single point. In MCZ 181165, the fibrous tissue beneath the orbit and lateral to the sphenoid is slightly calcified, giving the appearance of bony flanges ventral to the orbits.[8] The ventral surface of the sphenoid is without pronounced ridges except those bordering the posterior portion of its median ventral groove. The anterior Vidian foramina are barely within the lateral margin of the sphenoid. The trigeminal foramina are double on each side, separated by a prootic flange.

Hemipenial Morphology of Malagasy *Geodipsas*

I studied everted hemipenes of four species of Malagasy *Geodipsas* (*laphystia, zeny, boulengeri, infralineata*) and a retracted organ of *Geodipsas* species inquirenda (discussed in the species account for *boulengeri*). Thus, the only hemipenis left un-

[8] I have observed such calcified tissue in skulls of many colubrids and suspect it may be widespread. However, most preparations that are thoroughly cleaned do not show this feature. When present, such calcified tissue appears as translucent flanges lateral to the parasphenoid, and not part of the parasphenoid proper, which has a very distinct lateral border. In other colubrids, however, the parasphenoid has well-ossified lateral flanges underneath the orbits that are an integral part of the bone (e. g., *Xenodon severus*, MVZ 163319; *Psammophis sibilans*, MCZ 53438). Whether or not these two types of parasphenoid flanges are homologous is unclear, but my impression is that the latter type is usually situated somewhat more posteriorly than the former.

studied is that of *G. vinckei,* a species known only from the type. I describe the organs of the first four species here. That of *Geodipsas* species inquirenda will be described in a separate report dealing with that species; however, its hemipenis is very similar to the hemipenis of *Geodipsas boulengeri,* with which it has been confused.

With a view toward broadening the basis of comparisons of these snakes with their African congeners, I also studied hemipenes of all three African species of *Geodipsas.* I first present descriptions of the Malagasy species, followed by a summary of their similarities and differences *inter se.* This is followed with a similar treatment for the African species. Finally, I compare the morphology of hemipenes of the Malagasy and African species.

Geodipsas laphystia *(MCZ 181152, Everted; Fig. 14).* (See also the discussion of hemipenial spine mineralization in the *Remarks* appended to the description of *laphystia.*) The hemipenis is single (nonbilobed), noncapitate, acalyculate; proximally nude on the sulcate side (proximally spinose on asulcate side), with a midsection bearing enlarged hooked spines on the sulcate and "lateral" sides (small spines on asulcate side), and spinulate distal tip; sulcus spermaticus centrolineal and forked distally. The everted organ has a total length of 10 mm and a somewhat bulbous midsection and is slightly tapered at each end. The sulcus spermaticus is a deep furrow that forks 7 mm from the base (hence, forked approximately 3 mm, or about 30% its length). The branches are broad open grooves bordered with spinules; the tip of each branch stops short of the apex of the everted organ, which is entirely covered with long spinules.

The sulcate surface is proximally nude, with spines beginning approximately ⅓ of the way toward the tip, and continuous thereafter. Proximal spines are large, hooked, and robust, but they quickly grade into much smaller, narrow, straight spines or spinules. Beginning at approximately the point of sulcus division the spines gradually become longer toward the tip (those at the apex longer than many of the small hooked spines around the midsection).

Between the sulcate and asulcate surfaces, the "lateral" surfaces of the organ bear small spines proximally and a dense battery of enlarged hooked spines on the lower midsection; these latter grade gradually into small straight spines distally.

The asulcate surface bears two very large hooked spines basally; these are positioned mesially on the asulcate surface and are the largest spines on the organ. These two spines are surrounded by a sparse array of small, slightly hooked spines. The small spines lengthen gradually and become straighter distally, occupying the entire asulcate surface except for a "lateral" series of three to four enlarged hooked spines on the lower midsection (these comprise the line of "lateral" hooked spines closest to the asulcate side).

Geodipsas zeny *(MCZ 181161, Everted; Fig. 15).* The hemipenis is single (nonbilobed), noncapitate, acalyculate; proximally nude, with a spinose midsection, and distally spinulate; sulcus spermaticus centrolineal and forked distally. The everted organ has a total length of 7 mm a somewhat bulbous midsection and is slightly tapered at each end. The sulcus spermaticus is a deep furrow that forks 5 mm from the base and has a total length of 6 mm (hence, forked approximately 1 mm, or about 17% of its length). The branches are broad open grooves bordered with spinules; each branch stops well short of the apex of the everted organ, which is covered with spinules.

On the midsection of the sulcate side is a battery of spines (but not a dense array), including a pair of enlarged spines proximally, with more distal spines only about ½ as large. The spines grade into spinules, which densely cover the tip of the organ, beginning slightly proximal to the level at which the sulcus forks. The distal spinules are longer than proximal ones. The base of

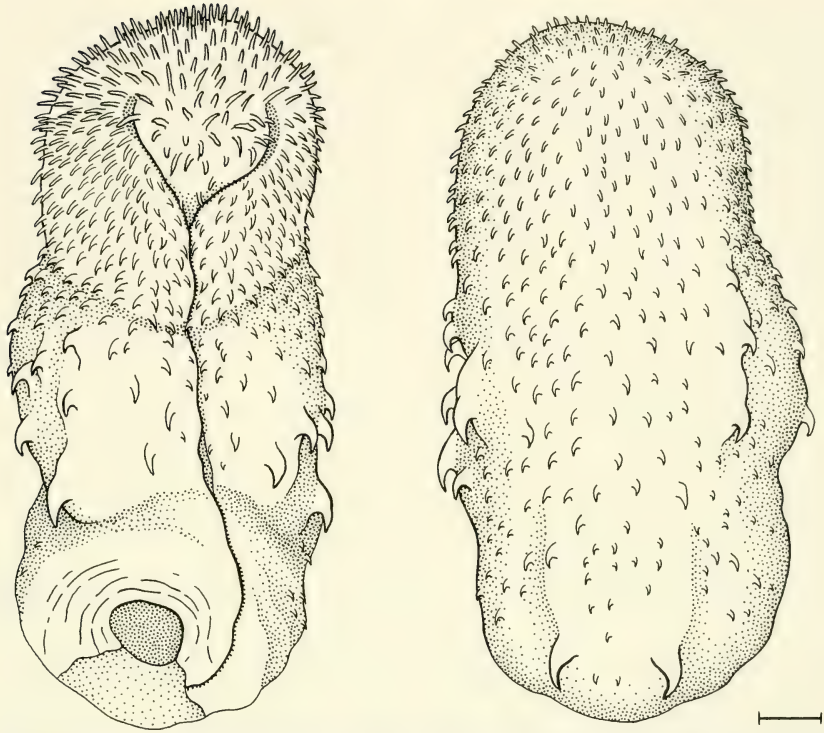


Figure 14. Hemipenis of *Geodipsas laphystia* (MCZ 180342; specimen from the RNP). Fully everted organ in sulcate (left) and asulcate (right) views.

the organ on the sulcate side is largely nude.

On the base of the asulcate side is a pair of enlarged, hooked spines, somewhat irregularly placed; other smaller spines occupy a median raised longitudinal lobe. Intervening spaces among these spines are nude or with minute hooked spines. The surface tissue of the asulcate side is slightly folded into several irregular longitudinal folds such that a couple of the enlarged spines appear to sit upon a flap comprising these folds. Distally the organ is densely spinulate, with spinules arrayed indistinctly in longitudinal rows; they become gradually longer and denser toward the tip. The distal tip of the organ is flexed toward the sulcate side and bears long, straight spinules.

Geodipsas zeny *(BMNH 95.10.29.62, Retracted).* The retracted hemipenis of BMNH 95.10.29.62 was studied through a previous incision. The organ extends to the middle of the sixth subcaudal; the sulcus spermaticus divides at the middle of the fifth subcaudal and the branches extend virtually to the apex of the organ. The major retractor muscle of the hemipenis is divided for approximately 1 mm at its attachment to the organ. The ornamentation

of the organ is like that just described for the everted condition. A band of enlarged hooked mineralized spines extends across the midsection of the hemipenis; this band is approximately two to three spines in width, but distally these grade imperceptibly into the spinulate distal section. The asulcate surface of the organ is strongly pleated into thick longitudinal folds upon which sit the large hooked spines ornamenting the organ. These folds occupy nearly the entire length of the inverted organ. The basal ⅓ of the organ is nude.

The folds visible in the retracted organ of *Geodipsas zeny* remain visible upon eversion (Fig. 15) but do not have the appearance of solid cords of tissue in the everted organ. Rather, they appear to be loose folds in the surface tissue and, thus, are very different from the solid ridges present in the hemipenis of *Geodipsas depressiceps* (see later).

Geodipsas boulengeri *(MCZ 181163, Everted; Fig. 16).* The hemipenis is single (nonbilobed), noncapitate, and acalyculate; proximally nude, with a spinose midsection, and distally spinulate. Sulcus spermaticus centrolineal, terminally forked, but the forked portion is so short that the distal tip of the sulcus merely appears to have a broad expansion; this appearance results from the sulcus ending distally essentially at the point of branching, hence somewhat broader than the more proximal portion. The sulcus is approximately 6 mm in length, the terminal division <1 mm. The tips of the sulcus branches stop well short of the apex of the everted organ (2 mm from the apex), which is covered densely with spinules. The everted organ has a total length of 9 mm. The distal tip of the organ is flexed toward the sulcate side.

A large protruding hemispherical lobe is present basally (Fig. 16). The distal surface of the lobe is covered sparsely with tiny spines; the proximal surface is nude.

The midsection of the organ bears a battery of moderately sized, hooked spines arrayed in a band approximately three spines wide and extending from the sulcus to the lateral portions of the asulcate side. Approximately 12–15 spines are on each side of the organ; distally the spines grade rather abruptly into long, narrow spinules, which densely cover the tip of the organ. The sulcus forks distal to the spinous midsection just within the spinulate area. Immediately distal to the sulcus is a pair of deep dimples in the surface of the organ, separated by several rows of densely packed spinules. The dimples appear to be small nude areas nestled deeply among the long, densely packed spinules in this region. The base of the organ on the sulcate side below the spinous midsection is entirely nude.

The asulcate side bears two large, hooked spines basally, slightly asymmetrically placed and of slightly different sizes (the smallest of these two approximately equal in size to the largest spines in the battery around the midsection). Proximal to these spines, the asulcate surface is nude. A broad protruding longitudinal lobe extends from the basal spines along the midline of the asulcate side, ending short of the tip of the organ (occupies approximately the middle ½ of the length of the organ). Entire asulcate surface distal to the basal spines, including the longitudinal lobe, ornamented with small hooked spines, distally grading gradually into spinules. The spinules are much longer on the sulcate than on the asulcate side.

Geodipsas infralineata *(MCZ 181153, Everted; Fig. 17).* The hemipenis is single (nonbilobed), noncapitate, and acalyculate; proximally more or less nude, having a spinose midsection, and distally spinulate; sulcus spermaticus centrolineal and forked distally. The everted organ is strongly flexed toward the sulcate side (probably due to contraction of the major retractor muscle internally) and has a total length of approximately 23–24 mm measured along the outer (long) flexure. The sulcus spermaticus is a deep furrow with a total length of approximately 12 mm; it forks distally, each branch of the fork approxi-

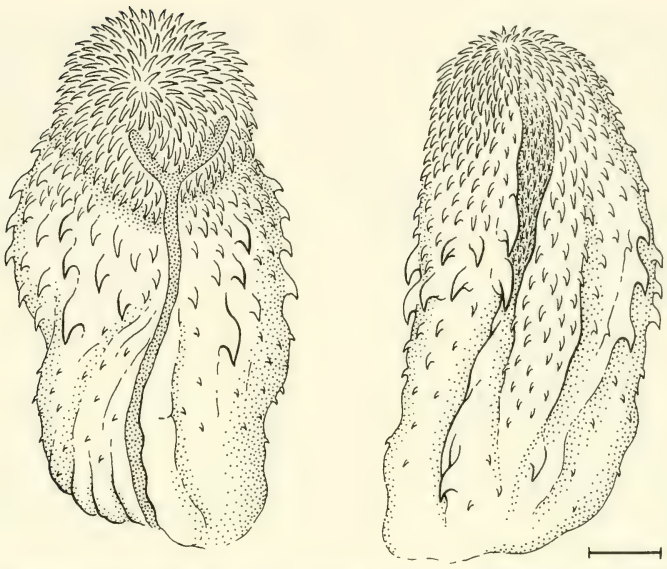


Figure 15. Hemipenis of *Geodipsas zeny* (MCZ 181161 [holotype]; specimen from near Midongy du Sud). Fully everted organ in sulcate (left) and asulcate (right) views.

mately 2.5 mm long (approximately 21% forked). The branches are broad open grooves bordered with spinules. The proximal undivided portion of the sulcus and the proximal portion of the forks is a closed canal formed by the appressed lips of the sulcus. The distal tips of the forks are open grooves that are somewhat flared and rounded distally (in form rather like elongate teardrops).

To investigate the nature of the major retractor muscle, the contralateral everted organ of MCZ 181153 and a single everted organ each of MCZ 181154 and MCZ 181157 were incised. The retractor muscle is terminally divided at its internal attachment to the organ.

The midsection of the sulcate and "lateral" sides bears a battery of moderately sized hooked spines, approximately 15–20 on each side, that increase gradually in size from the sulcate toward the asulcate side. Scattered among these spines are minute hooked spines that are clearly visible only under high magnification. The spines grade into long, narrow spinules, which densely cover the tip of the organ beginning slightly proximal to the level at which the sulcus forks. The distal spinules are longer than proximal ones. The base of the organ below the spinous midsection is largely nude, but minute spinules border the proximal portion of the sulcus spermaticus.

The midsection of the asulcate side bears two longitudinal rows of greatly enlarged, hooked spines, the rows slightly diverging and each having four spines. Within each row the two proximal spines are the largest, the third is somewhat smaller, and the distal spine is about ½ the size of the third. The distal spine is approximately the same size as the adjacent spines of the battery extending from the sulcate side.

The area between the rows of spines bears minute spines or spinules. Basally, there is a single moderate-sized spine (much smaller than those in the diverging rows) placed asymmetrically toward what would be the lateral side of the retracted organ; otherwise, the base of the asulcate side is mostly nude (scattered minute spinules). Distally the spinous midsection grades into the spinulate tip, the density and length of spinules increasing distally and toward the sulcate side (densest in the region around the sulcus forks). The spinules are in roughly longitudinal rows that converge around the tips of the forks of the sulcus spermaticus.

The surface tissue of this organ lacks pleats or an irregular surface texture as in *boulengeri* and *zeny*.

Comparison of Hemipenes of Malagasy Species of *Geodipsas*

Hemipenes of all Malagasy *Geodipsas* (hemipenis of *G. vinckei* unknown) are nonbilobed, noncapitate, and acalyculate. Other common features include enlarged hooked spines on at least the midsection (nude or with minute spines proximally); long, densely arranged spinules distally; a centrolineal sulcus spermaticus that divides distally; and a major retractor muscle that has a very short division at its insertion.

Of these shared characters, two are putatively derived and distinguish *Geodipsas* from most other Malagasy colubrids: (1) a simple (nonbilobed) hemipenis and (2) relatively distal or terminal division of the sulcus spermaticus. The alternative plesiomorphic states for these characters are a divided (bilobed) organ and a more deeply divided sulcus spermaticus (see Myers and Cadle, 1994:27–28, for discussion and further references). Each derived state has apparently arisen independently many times within colubrids, as indicated by their restricted presence in diverse clades worldwide (e.g., in some genera of neotropical "xenodontines" [Cadle, 1984a] and broadly among colubrines [Cadle, 1984b, 1994]). That the simple organ of *Geodipsas* is derived from a primitively bilobed condition is suggested by the divided insertion of the retractor muscle in the four species studied herein (see Myers, 1973, 1974, for discussion). The nonbilobed hemipenis, the distally divided sulcus spermaticus, and general detailed similarity in form and ornamentation are the most persuasive indications that the Malagasy species of *Geodipsas* are a broadly monophyletic group. However, nonbilobation is also a shared feature with at least one other Malagasy colubrid genus (see later).

Considering the relative length of the terminal division of the sulcus spermaticus, the Malagasy species of *Geodipsas* can be arrayed in a morphocline, as follows (from relatively more plesiomorphic to more derived; percentage division of sulcus in parentheses): *laphystia* (30%) > *infralineata* (21%) > *zeny* (17%) > *boulengeri* and *Geodipsas* species inquirenda (< 17% each; in both species the sulcus appears barely divided [see Fig. 16], but accurate measurement is difficult on such small organs).

Cadle (1996:442–443) called attention to an unusual structure of the sulcus spermaticus in species of *Liopholidophis* and Malagasy *Geodipsas*. In both of these genera, the sulcus is very broad and deep in comparison to the sulcus in other colubrids examined (primarily Neotropical, but also representatives of most genera of Malagasy colubrids). In form it resembles an open trough rather than a discrete groove or line on the surface of the organ, as in other colubrids. Quantifying the difference is difficult because accurately measuring sulcus depth is problematical. However, some comprehension of the *Geodipsas* condition is offered by the observation that the sulcus in the specimen of *zeny* examined is nearly 1 mm deep on an organ whose overall diameter at the widest point is only about 3 mm. In the retracted organ, the sulcus is deep, with a smooth bottom,

Figure 16. Hemipenis of *Geodipsas boulengeri* (MCZ 181163; specimen from the RNP). Fully everted organ in sulcate (left) and asulcute (right) views.

and surrounded by thickened fleshy ridges. The taxonomic and functional significance of this structure is, as yet, unclear.

Details of hemipenial morphology of all four described species of Malagasy *Geodipsas* are very similar. Although the organ of *infralineata* is strongly flexed (Fig. 17), and therefore appears different in configuration than the other species, this could be a preparation artifact. Aside from this, the ornamentation of the *infralineata* organ is similar to the other species. At first glance, the prominent diverging rows of greatly enlarged spines on the asulcate surface in *infralineata* seems unique among the species of *Geodipsas*. However, they also are manifested in the organs of *laphystia, zeny,* and *boulengeri,* although in these species the spines are much less prominent and they number only two or three in a row (Figs. 14–16). Thus, the distinctiveness of the asulcate spine arrangement is not as apparent as it is in *infralineata.*

In having *two* enlarged basal spines on the asulcate side (Figs. 14–16), the hemipenes of *laphystia, boulengeri,* and *zeny* differ from those of *infralineata,* which has only a single spine. This does not seem to be an artifact of the organ of *infralineata* described because the contralateral organ of the same specimen, as well as both organs of three other specimens, had a single spine; however, one specimen of *infralineata* (MCZ 181157) did have a second minute basal spine on both organs in the same position as the second spine in organs of the first three species. The basal spine "missing" in *infralineata* compared to the other three species would be mesial in position in the retracted organ.

Aside from minor ornamentation differences, the only seemingly unique feature of the hemipenes among the four species

of Malagasy *Geodipsas* is the basal spinose lobe to one side of the sulcus in *boulengeri* (Fig. 16). This may be approached by a somewhat similar-appearing spinose bulge in the same position on the organ of *laphystia*.

Hemipenial Morphology of African Species of *Geodipsas*

Bogert (1940) described the hemipenis of *Geodipsas depressiceps*, the first described for any member of this genus. Rasmussen et al. (1995) gave cursory characterizations for the hemipenes of *G. vauerocegae* and *G. procterae* but provided no details on ornamentation. I amplify these descriptions here and compare the hemipenes of African and Malagasy species of *Geodipsas*. My observations of African species are based on examination of an *in situ* retracted and an everted organ of *G. vauerocegae*, an *in situ* retracted organ of *G. procterae*, and an *in situ* retracted organ and an everted organ (using the method of Pesantes [1994]) of *Geodipsas depressiceps*.

Geodipsas vauerocegae *(MCZ 23289 and MCZ 23281, Everted and Retracted, respectively).* The hemipenis is nonbilobed, acalyculate, and with large hooked spines from near the base to the tip of the organ. The sulcus spermaticus divides approximately at or slightly distal to the midpoint of the everted organ, with the branches extending to the tip on the same side of the organ (centrolineal in orientation). The retracted organ extends to the suture between subcaudals 8–9. The sulcus divides at approximately the suture between subcaudals 4–5 (thus, approximately 50% divided). The tips of the branches in the retracted organ end virtually at the apex. The everted organ is 9–10 mm total length, the sulcus dividing 5 mm from the base.

The sulcus spermaticus is bordered by prominent fleshy lips. Beyond the point of branching, the individual branches continue as deep grooves partly obscured by overhanging tufts of spines or spiny papillae; each branch ends in a separate nude area (further described later) on the apex of the organ.

The tip of the hemipenis has an unusual ornamentation. The tips of the branches of the sulcus end in separate nude areas delimited and separated by tufts of spiny papillae: a large tuft between the branches of the sulcus on the sulcate surface, a smaller pair of tufts situated at the distal tip of the organ on the asulcate side (one tuft symmetrically placed on each side), and a large ridge of spiny papillae extending from the sulcate to the asulcate side and separating the distal nude areas from one another. In the corresponding retracted organ of *G. vauerocegae*, the distal nude areas appear as expanses of somewhat pleated tissue separated by tufts of spiny papillae.

The entire body of the organ is ornamented with hooked spines. These are small on the proximal ⅓ of the organ, with the remainder having larger hooked spines. The spines are robust, have thick fleshy-looking bases, and on the body of the hemipenis are arrayed in rather regular oblique rows. Spines in large patches (each containing 25–30 spines) on either side of the sulcus spermaticus and "sides" of the organ are larger than those on most of the asulcate side. A patch containing seven to eight enlarged spines is placed mesially at the base of the asulcate side. Aside from these differences there is little proximodistal or sulcate/asulcate difference in the density of spine distribution (except apically), although there is slightly greater basad extension of the enlarged spines on the sulcate and asulcate than on the "lateral" sides. The area between the forks of the sulcus is occupied by large spines overhanging from the apical tuft of spines in this region.

Geodipsas procterae *(MCZ 20188, Retracted).* The hemipenis is nonbilobed, acalyculate, and with large hooked spines from near the base to the tip of the organ. The retracted organ extends to the suture between subcaudals 10–11. The sulcus

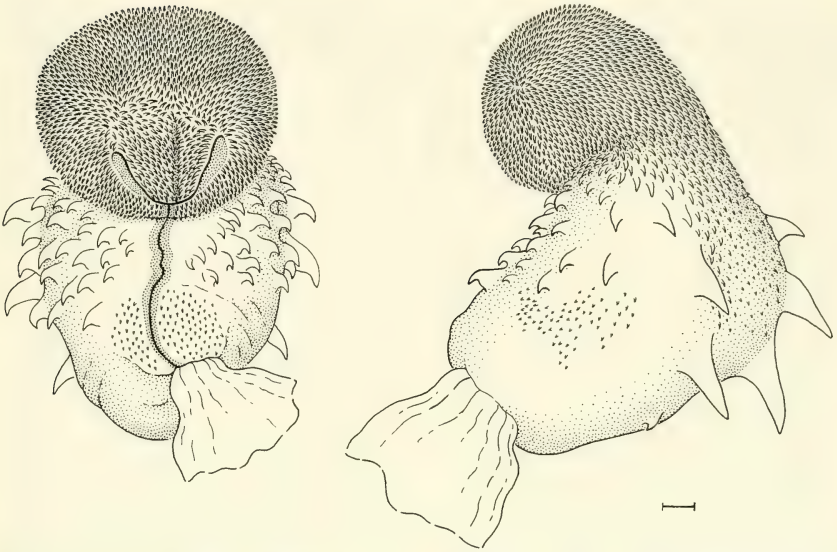


Figure 17. Hemipenis of *Geodipsas infralineata* (MCZ 181153; specimen from the RNP). Fully everted organ in sulcate (left) and asulcate (right) views. The asulcate view is shown in three-quarters view to accommodate the strong flexure of this particular organ. The flared tissue at the base of the organ is simply the tissue below the ligature tying off the base.

spermaticus divides at the suture between subcaudals 4 and 5 (approximately 65% divided) and extends distally in the lateral wall of the retracted organ (centrolineal in orientation); the branches extend to separate nude areas on the apex of the organ. The spines are much denser on the sulcate than on the asulcate side, are present between the branches of the divided sulcus, and appear to be arranged roughly into longitudinal rows. The form of the spines and the relative distribution of spine sizes appears similar to that described for *G. vauerocegae,* including the presence of a patch containing seven to eight enlarged spines basally on the asulcate side. As in *G. vauerocegae,* the sulcus branches end in nude areas separated by tufts of spines, although the nude portions seem less extensive than in *vauerocegae* (but perhaps would be equivalent upon eversion). The distal ornamentation, spine size and distribution, and overall appearance of the hemipenis of *G. procterae* are probably very similar to that of *G. vauerocegae* in the everted state.

Geodipsas depressiceps *(MCZ 9261, Retracted and Everted).* Bogert's (1940: 38) description of the hemipenis of *G. depressiceps* (based on a specimen from the Congo) is here repeated in its entirety: "Not bifid [i.e., nonbilobed], extending to the seventh caudal, but with the sulcus bifurcating at the second. Near the base are about thirteen slightly enlarged basal hooks in a V-shaped arrangement, with the apex distally at the sulcus immediately anterior to its division. From each basal hook there extends a ridge surmounted with spinules, the ridges becoming less apparent at the distal end, which is ornamented with slender spines."

My observations of MCZ 9261 (from Cameroon) agree essentially with Bogert's,

but I add a few details. The retracted organ of MCZ 9261 extends to the middle of subcaudal 6 and the sulcus spermaticus bifurcates at the level of the suture between subcaudals 2 and 3. The everted organ is approximately 6.2 mm in length (with some of the base damaged during eversion); the sulcus divides at about 1.5 mm (i.e., sulcus divided for about 65–70% of its length, the same proportion as on the organ that Bogert [1940] studied). The sulcus spermaticus, including the divided portion, is centrolineal in orientation, and its branches extend to the apex of the organ in both the retracted and everted state; there, the branches end amid tufts of spines.

Approximately 25% up from the base of the organ, a ring of slightly enlarged, hooked spines encircles the hemipenis (reaching somewhat more distally adjacent to the sulcus than asulcate side; this results in the "V-shaped arrangement" in the retracted organ observed by Bogert). Small spines ornament the portion of the organ proximal to this ring. The body of the organ is ornamented with thickened ridges that bear small spines at their apexes; these ridges mostly extend from the slightly enlarged basal spines, as observed by Bogert. There are approximately 10 such ridges in MCZ 9261. Three of the ridges are more prominent than the others: the pair bordering the outer edges of the sulcus spermaticus, and the ridge separating the branches of the sulcus from its point of division to the apex. Although single for most of its length, the latter ridge distally divides into two portions that parallel the respective sulcus branches. Dense arrays of long, narrow spines occupy the longitudinal strips of tissue between the ridges; these are more or less straight or have bent tips. Adjacent to the base of the sulcus is a discrete series of three or four short folds of tissue that are covered with a dense array of small hooked spines. Similar spines generally cover the base of the organ proximal to the encircling ring of enlarged hooked spines.

The most important new observation here concerns the nature of the ridges and ornamentation. Each ridge is composed of a more or less solid cord of tissue proximally but tends to become subdivided distally into more or less oblique pleats. In the retracted organ, one ridge on the asulcate side is distally produced into rather broad, more or less transverse pleats resembling flounces, although these are less extensive than is usually connoted by that term; these pleats are interconnected by ridges of tissue, giving the appearance of loose calyces. In the everted organ, the pleats disappear and are seen merely as slightly overlapping folds of tissue. Slender spines with bent tips project from the sides and apex of each ridge.

Each ridge has the appearance of having been formed by the fusion of the bases of enlarged spines originally arranged into longitudinal rows. This derivation is suggested by the small spines that surmount the ridges, as if only the tips of originally separated elongate spines are exposed above the fused tissue comprising the ridges. Moreover, with high magnification and proper lighting, the bases of individual spines comprising the ridges can be seen as denser areas of tissue. In addition to the spines on the ridges, long, narrow spines occupy the longitudinal strips of tissue between the ridges.

Comparison of Hemipenes of African Species of *Geodipsas*

The hemipenes of all three African species of *Geodipsas* are nonbilobed, acalyculate, and ornamented with spines from the base to the tip. The sulcus spermaticus is deeply divided in all three species (50% in *Geodipsas vauerocegae*, 65–70% in *G. procterae* and *G. depressiceps*). The branches of the divided portion of the sulcus in all three species diverge slightly and end at the apex of both retracted and everted organs; the orientation is centrolineal. *Geodipsas vauerocegae* and *G.*

procterae share more hemipenial characters than either does with *G. procterae.*

Aside from the more deeply divided sulcus spermaticus in *Geodipsas procterae,* the hemipenes of *G. vauerocegae* and *G. procterae* are very similar. The distal ornamentation of the lobes, including nude expanses separated by tufts of spines, is a peculiar, probably derived, similarity shared by these two species. Moreover, the distribution of spines is similar in these two species, including patches of enlarged spines adjacent to the sulcus and a small patch of enlarged spines basally on the asulcate side.

In contrast, the hemipenis of *G. depressiceps,* with its series of peculiar longitudinal ridges, basal spiny folds adjacent to the sulcus, and encircling ring of basal hooked spines, is rather different from the other two African species. Whereas the everted hemipenis of *depressiceps* is dominated by the longitudinal spiny ridges, no features resembling those are seen in either *vauerocegae* or *procterae.* I detected no detailed similarities in ornamentation between *depressiceps* on the one hand, and the two east African species of *Geodipsas* on the other, that suggest a special relationship between these two groups of species.

The overall form of individual spines also differs between *vauerocegae* and *procterae* on the one hand and *depressiceps* on the other hand. Except for the basal ring of spines, in *depressiceps* the spines are long, narrow, and either more or less straight or (more frequently) bent at the tip. In the former two species, the spines are short, thick, and strongly hooked and have thick, somewhat fleshy-appearing bases. The differences in spine morphology alone result in quite different superficial appearances of the hemipenes of *vauerocegae* and *procterae* compared to *depressiceps.*

The special hemipenial similarities (i.e., apical morphology and patterns of spine distribution) shared by *Geodipsas vauerocegae* and *G. procterae,* as well as their shared detailed similarity in spine morphology and their biogeographic proximity relative to *depressiceps,* suggest that *vauerocegae* and *procterae* are closest relatives. Of course, whether or not these three species of African colubrids are a monophyletic group remains an open, and much larger, question that is not specifically addressed here (but see later comments). No hemipenial characters preclude this hypothesis being correct, despite the strong differences in morphology between *depressiceps* and the other two species. However, other than the nonbilobed overall morphology of the organs, no clearly apomorphic hemipenial characters were identified that support the monophyly of these three species. Discovery of other African colubrids sharing putatively derived features with one or more species of African *Geodipsas* (e.g., nonbilobation, peculiar ridges, or apical structures) will require reconsideration of this question.

Comparison of Hemipenes of African and Malagasy Species of *Geodipsas*

The hemipenes of African *Geodipsas* are similar to the Malagasy species in being nonbilobed (simple) and having a divided sulcus spermaticus that is centrolineal in orientation. Otherwise, the details of structure and ornamentation are rather different in the two geographic groups.

In the Malagasy species, enlarged, hooked spines are sparsely distributed basally and around the midsection of the organ, but distally these grade abruptly into long, more or less straight spinules that densely cover the distal tip of the organ. Thus, the distal ornamentation of the organs in the Malagasy species is quite different from the more proximal ornamentation (see Figs. 14–17), resulting in a distinctively ornamented head region. In the African species, enlarged hooked spines cover the entire surface of the hemipenis (*vauerocegae* and *procterae*), or the body of the organ is covered with longitudinal, spine-bearing ridges (*depressiceps*). Al-

though in *vauerocegae* and *procterae* the tip of the hemipenis bears nude regions where the branches of the sulcus terminate, no distinctively ornamented head region occurs.

The African and Malagasy species of *Geodipsas* also differ in several aspects of the morphology of the sulcus spermaticus. The terminal divided portion is shorter in the Malagasy species (≤30% the length of the sulcus) than in the African species (≥50%) (see preceding descriptions for details). More basal division of the sulcus spermaticus appears to be plesiomorphic within many clades of colubrids (reviews in Myers, 1973, 1974; Myers and Cadle, 1994). Increasingly distal division, or shortening of the individual branches to give the *appearance* of more distal division, is a derived state compared with basal sulcal division. Thus, in this respect the Malagasy species of *Geodipsas* are more derived than their African congeners.

Perhaps correlated with shorter sulci spermatici in the Malagasy species, the distal tips of their sulci invariably fail to reach the apex of the everted hemipenis (apparently a result of differential expansion of apical tissues upon eversion, as the sulci of retracted organs reach virtually to the apex). In all Malagasy species, the apex of the organ is densely covered with spinules; the tips of the sulcus spermaticus in everted organs stop well short of the apex. In contrast, the tips of the sulcus spermaticus in the the African species always reach the apexes of both retracted *and* everted organs.

Finally, the African species of *Geodipsas* do not exhibit the unusual "trough-like" morphology of the sulcus spermaticus shown by the Malagasy species (see *Comparison of Hemipenes of Malagasy Species of Geodipsas*). In *vauerocegae* and *procterae,* the relative depth of the sulci appears more or less "normal," although in both species well-developed lips border it. The structure of the sulcus in *procterae* is unusual in having prominent longitudinal ridges bordering it and another ridge separating its branches. In none of the African species does the sulcus appear as deep as in the Malagasy species.

At first glance, one feature of retracted organs of *Geodipsas depressiceps* and *G. zeny* appears similar: the retracted hemipenes of both species appear to have longitudinal ridges. The similarity is only superficial, however. The ridges in *depressiceps* are more solid and remain evident on the everted organ (especially those surrounding the sulcus). The "ridges" in *zeny* largely disappear in the everted hemipenis; they are created in the retracted state by simple folding of the expansible tissue of the organ.

Thus, there are few shared similarities between hemipenes of African and Malagasy species of *Geodipsas* that could be construed as synapomorphies. However, a problem in interpreting the morphology of these animals is the lack of a broader context insofar as most other snakes pertinent to the problem of *Geodipsas* monophyly is concerned. In comparing the hemipenial morphology of African and Malagasy species of *Geodipsas,* I was specifically concerned with identifying characters potentially interpretable as synapomorphies. This proved difficult because many of the hemipenial descriptions of African and Malagasy snakes in the literature are insufficiently detailed to be informative in a broad comparative context (a statement that applies equally or greater to some other character sets, such as osteological ones). This situation should improve as basic descriptive studies are completed; several papers by Domergue (1983, 1986, 1987) and Cadle (1996) are steps in this direction for Malagasy colubrids. Nonetheless, an enormous amount of this basic work remains to be done before the phylogenetic relevance of many hemipenial characters in these snakes becomes apparent. In the next section I try to put the hemipenial data available on African and Malagasy *Geodipsas* into perspective when considered in conjunction with other characters and taxa.

Relationships of *Geodipsas*

In this section I raise the issue of whether *Geodipsas sensu lato* is monophyletic and review characters that have been used to define the genus. I conclude that no strong evidence favors monophyly of the genus in the broad sense. I do not intend here to rigorously estimate the relationship of included species to other Malagasy and African snakes. Knowledge of most colubrid genera from these areas must substantially improve before such a critical assessment can take place. What follows is a provisional interpretation of similarities between the Malagasy and African species of *Geodipsas* and between the former and other species of Malagasy colubrids.

Analysis of the relationships of Malagasy species of *Geodipsas* is clearly complicated by the inclusion of three African species in the genus, although that seems to be largely for historical and rather arbitrary nomenclatural procedures (see later). The three African taxa involved are *Tropidonotus depressiceps* Werner (1897), *Geodipsas vauerocegae* Tornier (1902), and *G. procterae* Loveridge (1922). Their inclusion in *Geodipsas* seems almost accidental when the literature associating them with *Geodipsas* is examined. The basis for including both African and Malagasy species in the same genus (or even species within either of these geographic units) seems never to have been carefully considered. But the issue of whether *Geodipsas sensu lato* is monophyletic is of broader importance than simply resolving a taxonomic issue. *Geodipsas* is widely cited in distributional summaries of the Malagasy fauna as a "shared element" with Africa (e.g., Brygoo, 1987; Cadle, 1987). Yet, in the absence of strong evidence for the monophyly of the genus, it is not clear what such a statement means or, indeed, whether it has any meaning at all. In the following historical summary, I attempt to reconstruct the reasoning that led to inclusion of African and Malagasy species in *Geodipsas* and then evaluate whether that broad concept of the genus seems well supported.

Status of African Species. Boulenger (1896) erected *Geodipsas* for the two Malagasy species known at that time, *infralineata* and *boulengeri.* Both species were originally described in the Neotropical genus *Tachymenis* Wiegmann (1834) (type species, *T. peruviana*), from which they differ, among other things, in having hypapophyses on the posterior trunk vertebrae. The first African species of *Geodipsas* described, *G. depressiceps* (Werner, 1897), was originally placed in the genus *Tropidonotus.* Subsequently, Andersson (1901) described the first African snake assigned to *Geodipsas* as *G. mapanjensis* (currently a synonym of *depressiceps*). Andersson (1901:20) commented that [*G. mapanjensis*] "seems to come nearest to *Geodipsas Boulengeri,* (Peracca), from which however it is distinguished by the keeled scales, the single loreal, the two praeoculars, the colour, and the geografical distribution . . . ." Andersson's generic assignment was probably based solely on using Boulenger's (1896) key. So, too, was Tornier's (1902) generic assignment for *Geodipsas vauerocegae,* which was accomplished with the simple comment "[c]lose to *Geodipsas infralineata* Blgr., but no diastema between the grooved teeth and the solid maxillary teeth" (Tornier, 1902:703). Sternfeld (1908) recognized that *G. mapanjensis* was a synonym of *Tropidonotus depressiceps* and first used the combination *Geodipsas depressiceps*; however, his comments on this point and the generic status are as follows (Sternfeld, 1908:410; my translation):

> Through examination of the type specimens of the Berlin Museum I was able to ascertain that *Tropidonotus depressiceps* Werner is identical with *Geodipsas mapanjensis* Andersson. In fact, we are dealing with a *Geodipsas* species, as examination of the dentition shows. It may well be closest to *G. vauerocegae* described by Tornier from the Usambara [mountains]; however, it is sharply separated by the keeled scales in 19 rows (17 in *G. vauerocegae*).

Thus, Sternfeld's assignment presumably was based almost solely on the presence of grooved rear teeth. And although Loveridge (1922) stated, without presenting evidence, that *G. procterae* was "closely allied" with Malagasy *Geodipsas,* he prefaced his description with the less definitive phrase "[*i*]*f* included in this genus [*Geodipsas*]. . . , the generic description will have to be enlarged to include snakes with single as well as double subcaudals" (emphasis added).

All of these authors apparently assigned the African species to *Geodipsas* by using Boulenger's (1896) key and generic diagnosis (Loveridge [1922] did so explicitly) and therefore based their assessment on shared features of posterior hypapophyses, grooved rear fangs, undifferentiated anterior maxillary and mandibular teeth, smooth scales, round pupil, and cylindrical body (but see discussion of pupil shape herein). Thus, the monophyly of *Geodipsas sensu lato* has never been critically evaluated relative to other Malagasy and African colubrid genera. Most authors (e.g., Guibé, 1958; Underwood, 1967; Brygoo, 1987; Cadle, 1987; Rasmussen et al., 1995) have implicitly accepted its monophyly. However, it seems equally, or perhaps more, plausible that the Malagasy species of *Geodipsas* are more closely related to other Malagasy colubrids than they are to their African congeners.

Furthermore, the characters that "support" recognition of *Geodipsas sensu lato* actually constitute rather weak evidence of relationship. All of the shared features that have historically been used to link the African species with those of Madagascar are arguably plesiomorphic character states (posterior hypapophyses, homogeneous dentition), have evidently evolved multiple times within colubrids (grooved rear fangs), or are dubious indicators of relationship at this level (smooth scales, cylindrical body).

Only with Bogert's (1940) description of the hemipenis of *Geodipsas depressiceps* was knowledge of the internal anatomy of these animals advanced (see also Underwood, 1967). Nevertheless, hemipenial characters have not been used as evidence supporting the monophyly of *Geodipsas sensu lato* (e.g., Rasmussen et al., 1995) despite their general importance in colubrid systematics. Hemipenial morphology of all described species of *Geodipsas sensu lato* except *G. vinckei* is now known (see earlier; Bogert, 1940; Rasmussen et al., 1995), and the monophyly of *Geodipsas* can now be addressed using hemipenial characters.

As already suggested, one putatively derived hemipenial character—single (nonbilobed) organs—is shared by the African and Malagasy species of *Geodipsas.* It seems not to have been used as evidence supporting the monophyly of *Geodipsas* by any author, although it is perhaps less equivocally a derived character than any of the characters already listed. Nonetheless, nonbilobed hemipenes have evolved many times within colubrids (for reviews and additional references, see Myers, 1974; Myers and Cadle, 1994). Without additional corroborating synapomorphies, the nonbilobed hemipenial morphology shared by African and Malagasy species of *Geodipsas* is weak evidence of monophyly. Moreover, this character, among others, is shared with at least one other genus of Malagasy colubrids, *Alluaudina* (discussed later). Thus, by itself the nonbilobed character of hemipenes of African and Malagasy species of *Geodipsas* does not unambiguously support its monophyly.

Several other aspects of hemipenial morphology show no special resemblance between the African and Malagasy species of *Geodipsas.* First, the sulcus divides more distally (a derived condition) in the Malagasy species than in their African congeners. Second, the details of ornamentation of hemipenes of Malagasy species of *Geodipsas* are quite similar among the Malagasy species, and these are quite different from the African species (see relevant sections, earlier). The African species, in fact, fall into two groups based on hem-

ipenial morphology and it is questionable whether or not any aspects of hemipenial morphology support the hypothesis that they themselves are monophyletic.

Thus, the case for considering *Geodipsas* in the broad sense monophyletic seems especially weak, essentially supported only by the derived condition of overall hemipenial morphology (single, as opposed to bilobed). This character is further undermined as a potential synapomorphy for *Geodipsas sensu lato* because it is found in at least one other Malagasy colubrid genus, *Alluaudina* (discussed later). The phyletic unity of the Malagasy species of *Geodipsas,* on the other hand, is supported by detailed similarity in several aspects of hemipenial morphology and by their sharing (again, with *Alluaudina* among other Malagasy colubrid genera) of a broadly elliptical pupil, an unusual (? derived) pupil morphology (see later).

I conclude that improved clarity of the uncertainty surrounding relationship of the Malagasy species of *Geodipsas* to those of Africa is best served by removing the African species to another genus, the Malagasy *Geodipsas infralineata* being the type species of *Geodipsas* (Loveridge, 1957). At the least, this would require that a hypothesized "link" between the Malagasy and African reptile faunas based on species of *Geodipsas sensu lato* be specifically justified by phylogenetic inference, rather than by recourse to what appears, at present, to be a taxonomic artifact. However, no other name seems to be currently available for the African species, and I defer specific nomenclatural action to a future report so as to be able to provide a more rigorous diagnosis for the new taxon that must be defined. This conservative course for the present seems also dictated by the questionable monophyly of the three African species, as implied by strong differences in hemipenial morphology between the east and central African species. I next consider evidence suggesting that the Malagasy species of *Geodipsas* are monophyletic *inter se.*

Monophyly of the Malagasy Species of Geodipsas *and Comparisons with Other Malagasy Colubrid Genera.* The Malagasy species of *Geodipsas* are a superficially disparate assemblage of snakes. *Geodipsas laphystia* and *G. infralineata* are highly arboreal snakes,[9] whereas *G. zeny* and *G. boulengeri* are not (of the two specimens of *zeny* with collection data, one was on the ground, the other in a shrub). *Geodipsas boulengeri,* especially, has a body form typical of terrestrial or cryptozoic snakes (short tail ending in a sharp point, small head little distinct from neck). Thus, consideration of the evidence indicating monophyly of the Malagasy species of *Geodipsas* is worthwhile.

The strongest indications of monophyly of the species of *Geodipsas* are the two putatively derived hemipenial characters described earlier: (1) simple (nonbilobed) organs and (2) distal or terminal division of the sulcus spermaticus. Moreover, the detailed similarity of ornamentation of the hemipenes is corroborative evidence of the monophyly of the five species for which the hemipenes are known (all except *vinckei*), even though character polarity for these features is problematic. These details include (1) midsection with enlarged, hooked spines; (2) enlarged bas-

[9] The macrohabitat of *Geodipsas vinckei* is difficult to infer from the only known specimen, which is rather dessicated, thus making exact interpretation impossible. My examination of the specimen leads to slightly different conclusions than Domergue (1988). Domergue (1988:140) reported the body form as "cylindrical. " My impression is that the body is somewhat compressed and with angulate ventrals. Both characters are found in many arboreal colubrids, but the relatively small head and short tail are not generally characteristic of arboreal snakes.

I augment Domergue's (1988) description of the type with the following comments. The type is a male, as suspected by Domergue (verified by gonad inspection through a previous slit in the body wall). It has 18 prediastemal maxillary teeth (not 12, as stated by Domergue), a diastema approximately 1. 5× the width of the preceding tooth, and two deeply grooved fangs. The scale row reduction is by loss of row 4 or fusion of 3 + 4 at the level of ventrals 100 (left side) and 102 (right).

al asulcate spine or spines; (3) "head" of the organ with long spinules, distinctly different in ornamentation than more proximal portions; (4) tips of the sulcus branches falling short of the apex on the everted organ; and (5) deep, trough-like morphology of the sulcus.

Casual inspection of hemipenial morphology of other Malagasy colubrids (Cadle, 1996; Domergue, 1984, 1986; unpublished observations for *Dromicodryas, Ithycyphus, Lycodryas, Liophidium, Madagascarophis, Pseudoxyrhopus*) reveals no others with detailed similarity comparable to that shared among species of *Geodipsas*. On the basis of the two shared derived hemipenial characters, plus the detailed similarities in overall ornamentation (pending their examination in *Geodipsas vinckei*), I conclude that the Malagasy species of *Geodipsas* are a monophyletic group.

The two putatively derived hemipenial characters shared by species of Malagasy *Geodipsas* are unknown in Malagasy snakes other than *Geodipsas* and *Alluaudina*. According to McDowell (1987:40), *Alluaudina* [*bellyi*] has a nonbilobed, entirely spinose hemipenis, but the sulcus spermaticus is more deeply forked than species of *Geodipsas* with the exception of *G. depressiceps*, which has the most deeply forked sulcus of any species of *Geodipsas* (see earlier descriptions). *Alluaudina* differs from *Geodipsas* in having a high number (25) of strongly keeled dorsal scale rows and perhaps some subtle differences in body proportions. One additional difference noted in most of the literature on these snakes is pupil shape: round in *Geodipsas* and vertically elliptical in *Alluaudina* (e.g., Guibé, 1958:234). That difference is actually nonexistent insofar as Malagasy species of *Geodipsas* are concerned, as both they and *Alluaudina* have broadly elliptical pupils (see *Pupil Shape in* Geodipsas).

It seems clear that at least the nonbilobed hemipenial morphology shared by *Geodipsas* and *Alluaudina* is a potential synapomorphy suggestive of a relationship between these two genera—at least as suggestive in this case as for the monophyly of the Malagasy and African species of *Geodipsas*. Moreover, *Alluaudina* shares with Malagasy *Geodipsas* a broadly elliptical pupil, which seems to be a less common state in colubrids than the round condition seen in African *Geodipsas*. I have not personally studied the hemipenial morphology of *Alluaudina*, and no detailed descriptions are in the literature. Thus, I cannot comment on the details of ornamentation in that genus or how they might compare with *Geodipsas*. However, the species of Malagasy *Geodipsas* have a derived condition of the sulcus spermaticus—division occurring on the distal half of the organ—that is not seen in *Alluaudina* according to McDowell's (1987) observations. More detailed study and comparison of *Alluaudina* with *Geodipsas* should help clarify whether, indeed, there is a relationship between these two.

Relationships among Species of Malagasy Geodipsas. Tentatively accepting the monophyly of the six Malagasy species of *Geodipsas* based on shared details of hemipenial morphology, as already documented, I offer some speculations on relationships among them. It seems possible to adduce evidence that two sets of species pairs are clades relative to the remaining two species.

Geodipsas laphystia and *G. infralineata* share a suite of characters associated with arboreality, including (1) prehensile tail; (2) compressed body with angulate ventrolateral edge; (3) body attenuation, with a narrow "neck" and relatively greater mass shifted posteriorly; (4) tail relatively long; and (5) head relatively broad and very distinct from neck. They also share high numbers of ventral and subcaudal scales and are unusual among *Geodipsas* in being highly polymorphic in dorsal ground color, with the range of colorations being similar in the two species. These two species are also similar in having the most plesiomorphic condition of the sulcus spermati-

cus, which divides more proximally in these than in the other species. If we assume that arboreality is a derived ecology in this genus, then the morphological correlates of that macrohabitat would be synapomorphies for a clade comprising these two species.

Geodipsas boulengeri and the species referred to herein as *Geodipsas* species inquirenda share two highly unusual aspects of color pattern (see Fig. 8): (1) a large, light-colored postmandibular spot on the neck and (2) discrete light spots (often dark-bordered) on each upper and lower labial scale. They both also show the most derived condition of the sulcus spermaticus: in both species the division is terminal, so that the tip of the sulcus appears merely expanded (branches extremely short; see Fig. 16). In fact, their hemipenes overall appear nearly identical (unpublished observations). Because of their highly unusual nature, I consider the two color pattern features derived, as is the terminal division of the sulcus. Thus, three synapomorphies support a clade containing these two species. The other two species, *Geodipsas zeny* and *G. vinckei,* are not so easily placed based on present knowledge.

Geodipsas zeny shares with *G. boulengeri* a low number of ventrals and subcaudals and small body size. Its color pattern is a curious mosaic of that in three other species. In having a fine network of dark lines anteriorly that tend to form diagonals separated by two scale rows (Figs. 4–5), *zeny* is similar to the pattern in *infralineata,* in which the diagonals usually are present over the whole body (Fig. 10). All three specimens of *zeny,* and some specimens of *infralineata,* have dark lateral nape blotches (cf. Figs. 4–5, 10). In having dark longitudinal lines posteriorly on scale rows 3–4 and 5–6, and the vertebral row, *zeny* is similar to *laphystia.* Finally, as indicated in the description of *zeny,* two of three specimens (MCZ 181161, BMNH 95.10.29.62) have light spots on the upper and lower labials. Neither manifestation of labial spots is as striking in *zeny* as in either *boulengeri* or *Geodipsas* species inquirenda (although they are quite discrete in the BMNH specimen), but the appearance of such spots in *zeny* might be construed as an incipient manifestation of the more well-developed condition in the other two species. Moreover, all three specimens of *zeny* have a dusky gular region with light maculations, as in *boulengeri.* In hemipenial morphology, *zeny* is most similar to *boulengeri* but hemipenial differences among the species of Malagasy *Geodipsas* in general are slight. Thus, *zeny* seems to be an amalgam of characters expressed more individually in the other species.

Geodipsas vinckei has a somewhat compressed body (see footnote 8) and an angulate ventrolateral body edge, both features shown by *G. laphystia* and *G. infralineata.* However, the body form of *vinckei* does not appear as modified for arboreality as are the other two species (e.g., it has a relatively small head not very distinct from the neck, and it has a relatively short tail; see Domergue, 1988). *Geodipsas vinckei* also has light spotting on the upper labials reminiscent of those in *boulengeri*; however, the spots are not as consistently present on the supralabials in *vinckei,* and they are also present on the loreals, preoculars, and some of the postoculars, unlike in *boulengeri. Geodipsas vinckei, laphystia,* and *infralineata* are the largest species of *Geodipsas,* with males reaching 600 mm or greater total length (<400 mm for all other species). The incipient arboreal adaptations (if inferred correctly from the dessicated type) are possibly weak evidence associating *vinckei* with the clade containing *laphystia* and *infralineata,* but any such inference seems tenuous.

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SPECIMENS EXAMINED

The following abbreviations of collections are used in the text and in the list of specimens examined. As all specimens are from Madagascar, localities begin with the province. Coordinates are given for those localities that could be reliably localized. Bracketed information in localities are inferred political units (province and, where possible, fivondronana), coordinates, or updated names for towns. A useful reference for names of smaller political units within provinces (fivondronanas) is Brygoo (1971:36, map 4), although some must now be updated to reflect current name usage.

BMNH	British Museum (Natural History), London
MCZ	Museum of Comparative Zoology, reptile collection, Harvard University, Cambridge
MNHN	Muséum National d'Histoire Naturelle, Paris
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
MZUT	Museo Zoologica dell'Università di Torino [now incorporated as part of the Museo Regionale di Scienze Naturali di Torino], Torino

Geodipsas boulengeri (Peracca)

*[**TOAMASINA:** Fivondronana Moramanga]:* "Valle dell'Umbi (Andrangoloka)" [Valley of the Umbi River (Andrangoloka)] [= Andrangoloaka] [19°02′S, 47°55′E], MZUT R-1874 (*holotype*). ***FIANARANTSOA:*** "Pays Zafiminary" [east of Ambositra *fide* C. A. Domergue, in litt., who obtained the specimens from Dr. H. Pinon; approximately 20°30′S, 47°30′E; the Zafiminary [=Zafimaniry]are one of the Tanala tribes], MNHN 1986.1373–78. *Fivondronana Ifanadiana:* Talatakely, Ranomafana National Park, 1,000 m [21°16′S, 47°25′E], MCZ 181163. *[Fivondronana Ikongo]:* Along the Sahandrato River, upstream from Tsianovoha [= Tsianivoho; 21°57′S, 47°21′E], 600 m

(Angel, 1936:125), MNHN 1936.19 (holotype of *G. heimi* Angel).

Geodipsas infralineata (Günther)

NO SPECIFIC LOCALITIES: *[? FIANARANTSOA]:* "Eastern Betsileo." BMNH 1946.1.7.20 (erroneously noted as holotype of *infralineata,* as explained in the text; thus, the correct locality for this specimen is "Eastern Imerina"). *[? TOAMASINA]:* "Eastern Imerina," BMNH 95.10.29.52 (inferred correct *holotype,* as explained in the text, in which case the correct locality data are "Eastern Betsileo"). ***[ANTSIRANANA:*** Fivondronana Andapa]: Marojezy, alt. 300 m [14°26′S, 49°44′E], MNHN 1986.1391. ***[ANTANANARIVO:*** Fivondronana Manjakatompo]: Manjakatompo [19°20′S, 47°26′E], MNHN 1957.731. *[? Fivondronana Anjozorobe]:* Forêt NE d'Anjozorobe [? approx. 18°24′S, 47°52′E; the particular "Anjozorobe" of three identified is assumed to be the largest, most accessible town of that name], MNHN 1986.1392. ***FIANARANTSOA:*** *Fivondronana Ifanadiana:* Ambodimaharira, Ranomafana National Park, 1,200 m [approximately 21°18′30″S, 47°26′E], MCZ 181154. Ivalohoaka, Ranomafana National Park, approx. 1,040 m [21°17′50″S, 47°26′20″E], MCZ 181153. Along main course of Menarano River south of Ivalohoaka, Ranomafana National Park, 1,130 m [approx. 21°18′30″S, 47°26′20′E], MCZ 181155–56. Approx. 2.2 km (airline) SE Sahavondrona along Andranoroa River, 1,170 m [21°17′10″S, 47°21′20″E], MCZ 181157. Talatakely, Ranomafana National Park, 900–1000 m [21°16′S, 47°25′E], MCZ 181147, 181149. *[Fivondronana Ikongo]:* Vallée de la Sahandratao [=Sahandrato =Sahandranto; 22°12′S, 47°28′E], MNHN 1936.20. *Fivondronana Midongy du Sud:* Approx. 7 km SW (airline) Midongy du Sud [Midongy Atsimo], near Rianambo ("high waterfall") on Alapo River, 670 m elev. [23°35′S, 47°01′E], MCZ 181160. ***[TOAMASINA]:*** *Fivondronana Moramanga]* R[oute] N[ational] 2 (route Tamatave), MNHN 1978.91. Vers PR 60, route de Tamatave, MNHN 1978.93. Perinet [= Andasibe; 18°56′S, 48°25′E], MNHN 1978.90, 1978.92, 1978.94. Environs of Perinet, Anamalazaotra Forest [18°56′S, 48°25′E], BMNH 1930.2.2.14. Forêt d'Analamazaotra (E) [18°56′S, 48°25′E], MNHN 1947.7. ***[TOLIARA:*** *Fivondronana Tolanaro]:* Region de Fort Dauphin ["mountains north of Fort Dauphin" *fide* tag attached to specimen; approx. 24°30′S, 47°00′E], MNHN 1986.1390.

Geodipsas vinckei Domergue

[TOAMASINA: *Fivondronana Moramanga]:* Station de Pisciculture de Perinet-Analamazaotra [= Andasibe; approx. 900 m; 18°56′S, 48°25′E], MNHN 1977.818 (*holotype*).

Geodipsas species inquirenda

(These specimens were referred to *Geodipsas "heimi"* [= *boulengeri*] in their respective museum catalogs, but I consider them to represent a distinct species; see comments under *Distribution* in the *Geodipsas boulengeri* species account).

[ANTSIRANANA*: Fivondronana Antsiranana]:* Joffreville [=Ambohitra; 12°29′S, 49°12′E], MNHN 1986. 1379. Montagne d'Ambre (forêt basse) [=Ambohitra; 12°30′S, 49°10′E], MNHN 1978. 2786, 1986. 1380. Montagne d'Ambre [= Ambohitra; 12°30′S, 49°10′E], USNM 149836.

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The American Orb Weavers *Hypognatha, Encyosaccus, Xylethrus, Gasteracantha,* and *Enacrosoma* (Araneae, Araneidae)

HERBERT W. LEVI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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THE AMERICAN ORB WEAVERS *HYPOGNATHA, ENCYOSACCUS, XYLETHRUS, GASTERACANTHA,* AND *ENACROSOMA* (ARANEAE, ARANEIDAE)

HEBERT W. LEVI[1]

ABSTRACT. *Hypognatha* are tropical American orb weavers, presumed to be related to *Gasteracantha* on the basis of the shared wide, square carapace and elongate fourth femur. There are 38 species known, of which 30 (about 80%) are new (21% previously known, 79% new). Four species names, *coccinellina, cruciata, geometrica,* and *prospiciens,* are synonymized. Other presumed *Gasteracantha* relatives are illustrated and their distributions mapped: *Encyosaccus* with one species, and *Xylethrus* with six species, two of them new. Males of *Encyosaccus* and *Xylethrus* are described. Two *Xylethrus* names, *peruanus* and *trifidus,* are synonymized. The species-rich, worldwide genus *Gasteracantha* has only one American species and a single record of an African species found in Venezuela. There are six species of *Enacrosoma,* three previously named and three new species. Two species names, *leprosa* and *sexlobata,* are synonymized. *Glyptogona,* a Mediterranean genus, has frequently been confused with *Enacrosoma.*

INTRODUCTION

This work is another in a series of revisions of tropical American orb weavers. Earlier revisions were cited in Levi (1993b). Since that time, the following genera have been revised: *Carepalxis* and *Rubrepeira* (1992), *Neoscona* (1993a), *Lewisepeira* (1993c), *Kaira* (1993d), *Bertrana* and *Amazonepeira* (1994), *Acacesia* (Glueck, 1994), *Metazygia* (1995a), *Actinosoma, Spinepeira, Hingstepeira, Pronous, Spilasma, Micrepeira, Madrepeira,* and *Tatepeira* (1995b), and *Scoloderus* (Traw, in press).

Before this revision, only three species (*Hypognatha elaborata, H. furcifera,* and *H. scutata*) of the 11 names listed in catalogs of Roewer (1942) and Bonnet (1957) could be determined with the literature on hand. Yet it is astonishing how many specimens in collections have been determined and misidentified by arachnologists.

METHODS AND ACKNOWLEDGMENTS

Taxonomic publications must be short and to the point due to limited funds and time and because unnecessary data may confuse the diagnostic features of species and genera. It is most important to illustrate the diagnostic characters; descriptions can be kept to a minimum. Readers should remember that North American species briefly described by J. H. Emerton are generally recognizable; the multi-page descriptions and illustrations by A. Petrunkevitch often are not. Keyserling and the two Pickard-Cambridges generally made adequate illustrations and their species can be recognized. Descriptions by Thorell and Simon are difficult to use, and original specimens must be borrowed for accurate species recognition.

The methods used here were as described in Levi (1993b), but some additional comments are needed. Descriptions of the ocular quadrangle are from the outside of the curvature of the lens. Measuring the eyes was discussed in Levi (1993b). Distances between the eyes of the anterior row are expressed as diameters of the anterior median eyes (in profile); distances between eyes of the posterior row are given as diameters of the posterior median eyes (in profile). The height of the clypeus,

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

the distance between anterior median eyes and the edge of the carapace, is expressed in the diameters of the anterior median eye (Levi, 1993b, fig. 28f). These measurements are approximate.

Measurements of sternum, palp, and the shorter articles of shorter legs are not given. While some leg measurements are useful, elaborate measurements of detailed descriptions can be distracting. Taking leg measurements of araneids is difficult without taking the animals apart, which is to be avoided. Accurate measurements of leg articles can be taken only if the legs are amputated and measured flat. In *Hypognatha,* taking the measurement of the first femur and also carapace length was especially difficult. Some earlier American authors reported accuracy of measurements to three decimal points, an unreasonable level of accuracy not supported by the methods used.

Hypognatha carapace length is measured between the clypeus to the farthest point on the posterior margin (but does not include eye projections). The width is measured at the widest point on the thorax and at the widest place in the cephalic region (just behind the posterior lateral eyes). In the gasteracanthine genera, which have a swollen cephalic region, the widest place of the carapace in the cephalic region was measured. The total length of the abdomen, if measured, was taken along the midline.

Measurements are usually to one-tenth of a millimeter for large species; smaller ones are measured to one-hundreth of a millimeter.

Epigyna were temporarily mounted with Hoyer's medium to search for seminal receptacles. The ducts of the *Hypognatha* epigynum are translucent, perhaps flattened, and difficult to see. There were not enough specimens of most species to stain tissues and make dissections. But again, the value of such dissections is questionable in helping to determine the species. They might be useful for making cladograms.

Record citation is also variable. There is no need to give date of collections and collector for common species just to be consistent. The location helps with distribution, and the museum's initials are needed for checking the data. No collection information is provided here for *Gasteracantha cancriformis* because it is a very common, widespread spider species. If printed the locality data and records of the available specimens would fill half the pages of this manuscript.

The specimens used came from the following collections:

AC	A. Calixto, Bogota, Colombia
AMNH	American Museum of Natural History, New York, United States; N. Platnick, L. Sorkin
BMNH	Natural History Museum, London, England; P. Hillyard, F. Wanless
CAS	California Academy of Sciences, San Francisco, California, United States; C. Griswold, W. J. Pulawski, D. Ubick
CV	Carlos Valderrama, Bogota, Colombia
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards
HECO	Hope Entomology Collections, Oxford University, Oxford, England; I. Lansbury, M. Atkinson
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Est. Amazonas, Brazil
LNK	Landessammlungen für Naturkunde, Karlsruhe, Germany; H. Höfer
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; E. A. Maury, C. L. Scioscia
MCN	Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; E. H. Buckup, M. A. L. Marques
MCP	Museu de Ciências, Pontifícia Universidade Católica do Rio

	Grande do Sul, Porto Alegre, RS, Brazil; A. A. Lise
MCSNG	Museo Civico di Storia Naturale, Genova, Italy; L. Capocaccia, G. Arbocco
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, United States
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador; L. Avilés, Germania Estévez Jácome
MHNC	Museu de História Natural, Capão da Imbuia, Curitiba, Paraná, Brazil; L. Bittencourt
MLJ	Maria Luisa Jiménez, La Paz, Mexico
MNHN	Muséum National d'Histoire Naturelle, Paris, France; J. Heurtault, C. Rollard
MNRJ	Museu Nacional, Rio de Janeiro, Brazil; A. Timotheo da Costa
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; D. Silva D.
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil; P. Vanzolini, J. L. Leme
NRMS	Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Kronestedt
PAN	Polska Akademia Nauk, Warszawa, Poland; J. Prószynski, A. Slojewska, W. B. Jedryczkowski
SMIJ	Science Museum, Institute of Jamaica, Kingston, Jamaica; T. H. Farr
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States; J. Coddington, S. F. Larcher
ZMUC	Zoologisk Museum, Copenhagen, Denmark; H. Enghoff, N. Scharff
ZSM	Zoologische Staatssammlung, Munich, Germany

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TAXONOMIC SECTION

Hypognatha Guérin-Méneville

Eurysoma C. L. Koch, 1839: 117. Type species *Acrosoma scutatum* (Perty) by monotypy. Name preoccupied by Dejean (1831) for a beetle, as cited in Neave (1939b: 366).

Hypognatha Guérin-Méneville, 1840: 109. Type species by monotypy *Hypognatha feisthameli* from Cayenne [=*Hypognatha scutata*]. The gender of the name is feminine (Bonnet, 1957: 2257). Neave, 1939b: 738.

Eurycorma Thorell, 1868: 4. New name for *Eurysoma* C. L. Koch. First synonymized by Simon (1895b: 874).

Hypophthalma Taczanowski, 1873: 283. Type species by monotypy *Hypophthalma deplanata* Taczanowski. *Hypophthalma* first synonymized with *Hypognatha* by Simon (1895b: 874).

Calydna O. P.-Cambridge, 1874: 174. Type species by monotypy *C. prospiciens* O. P.-Cambridge [=*Hypognatha scutata*]. *Calydna* preoccupied by *Calydna* Doubleday for a lepidopteran (Neave, 1939a: 553). *Calydna* synonymized by Simon (1895b: 874).

Mutina O. P.-Cambridge, 1875: 231; 1881: 771. Replacement name for *Calydna*. The first citation, a footnote in Zoological Record, is not in Neave

(1940: 231). *Mutina* synonymized by Simon (1895b: 874).

Diagnosis. Abdomen with dorsum lightly sclerotized and a pattern of scutes, not otherwise found in American araneids (Figs. 17–19, 52, 55). Sternum with a posterior notch, holding a finger from the epigastric area (Figs. 1, 141), but there is no obvious stridulatory mechanism. Fourth femur elongated, almost equal to or as long as combined length of fourth tibia and tarsus and equal to or longer than first femur. Males with lateral eyes on the tip of a projection (Figs. 6–8, 28, 29).

A similar pattern of scutes on the dorsum of the abdomen is also found in some *Phoroncidia* (Theridiidae Levi, 1964). Unlike *Hypognatha, Phoroncidia* has the eye region projecting above the clypeus. A similar abdominal pattern is also found in *Testudinaria* (family affinity uncertain), which has a narrower carapace and abdomen than *Hypognatha.* It is also found in *Augusta* O. P.-Cambridge males and *Isoxya penizoides* Simon from Africa or Madagascar.

Description. Female. Color orange to orange-brown in alcohol. Abdomen with variable color pattern, often bold, often contrasting, but sometimes diffused, no two individuals of a species alike (Figs. 17–19). (Colors given in the descriptions, later, are those of the individual described.) Carapace only slightly longer than wide, its width behind the lateral eyes almost equal to or wider than width of thoracic region (Fig. 139). Anterior and posterior median eyes subequal, posterior medians at most 1.3 diameters of anterior medians. Lateral eyes about half diameter of anterior medians, anterior laterals often slightly larger than posterior. Anterior median eyes separated by less than their diameter to 1 diameter, posterior median eyes separated by less than one diameter to 1 diameter. Median ocular quadrangle almost square, often slightly wider behind. Height of clypeus 2.2 to 3.0 diameters of an anterior median eye (4 in *H. rancho*, only 1.4 in *H. saut*). Clypeus variable in males (Figs. 6, 28, 42). Abdomen as long as wide, sometimes wider than long, or slightly longer than wide, widest in anterior half, with dorsum lightly sclerotized. Venter with two large plates anterior to pedicel (Fig. 72). A ring, not sclerotized, around spinnerets. Carapace bald; few setae on legs and abdomen. All species are similar in size, females less than 4 mm. Only *H. cryptocephala* is slightly larger, to 5 mm.

Males smaller than females, total length about 3 mm or less. Carapace of adults with a pair of projections tipped by the lateral pair of eyes (Figs. 6–8, 28, 29). Anterior lateral eyes facing ventrally. Some species with modifications on clypeus (Figs. 28, 35, 42), a median projection (Figs. 146–148, 157–159) and grooves, which are probably held by the female fang's when mating (Figs. 28, 48).

Early instar females have notch on sternum and indications of abdominal scutes, but in males only adults have the carapace modifications; the last instar shows no sign of them.

Genitalia. Females with epigynum reduced and some with little sculpturing on venter of epigynal area (Figs. 142, 162, 165); some even have little sculpturing on posterior of the epigynum (Figs. 132, 135). Seminal receptacles bunched like grapes or a complicated coil (Figs. 4, 23, 34, 59). Internal ducts lightly sclerotized, flattened, and not readily discerned.

Males with heavily sclerotized palpi, in contrast to lightly sclerotized epigynum. Palpus appears slightly twisted with paracymbium (P in Fig. 15) one-third distant to distal margin of cymbium (Y in Figs. 11, 15). Conductor (C in Figs. 11, 12, 14, 16, 152) soft, fleshy, wider than long, broadly attached to distal margin of tegulum (T in Figs. 11, 12, 16, 152). Conductor supports only part of long embolus (E in Figs. 16, 152). Elongate sclerite, probably paramedian apophysis (PM in Figs. 12, 14, 16), proximal to conductor. Median apophysis (M in Figs. 12, 13, 16, 152, 227) variable, in many species soft, swollen, and extend-

ing proximally to palpus, sometimes with one or two spines pressed against its swollen body (Figs. 227, 228). This soft median apophysis is reminiscent of the median apophysis in *Eustala* species (Levi, 1977, m in fig. 232). Embolus (E in Figs. 10, 11, 13, 16, 152) with distal end thread-like, similar in all species, and with complicated base. Thread of embolus supported by median apophysis, conductor, and terminal apophysis (Fig. 16). Terminal apophysis (A in Figs. 10–13, 16, 152, 153) large, dissected, and variable in genus; often with distal coil (Figs. 152, 153). Palpus without distal hematodocha, terminal apophysis attached to base of embolus (Figs. 11, 16) and always supporting tip of embolus.

Palpal patella with one short, weak seta (not always found). Endite without tooth. First coxa with small hook on distal margin, and small, matching groove on second femur. Second femur sometimes with ventral, median, short macrosetae. Second tibia thicker than first and sometimes with similar macrosetae. Coxal hook and strong second femur reflect only slight differential size of male and female; however, tooth on endite lost.

Relationship. The scutes of the abdomen, the sternum with notch holding an abdominal projection, and the twisted bulb of the palpus are autapomorphies for *Hypognatha.*

The wide cephalic region of the carapace and the almost square carapace resemble those of *Gasteracantha* (probably a synapomorphy). The presence of a terminal apophysis in the palpus and the complicated sclerites are plesiomorphic. *Hypognatha* species have a ring around the spinnerets, but the ring is not sclerotized (Table 1).

Distribution. Hypognatha is only known from tropical America, most species from the Amazon area (Maps 1, 2).

Natural History. The web of *H. mozamba* has been illustrated (Eberhard, 1986, fig. 4.2e). "Their webs are relatively flimsy, built in very large open spaces around dusk, and do not last very long before becoming quite tattered. The spiders seem to tear them down only a few hours after they have put them up" (Eberhard, personal correspondence, May 1995).

Misplaced Species. Bonnet's catalog (1957: 2258) lists the African *Eurysoma vicina* Blackwall (1866: 465) in *Hypognatha.* This species is listed in *Paraplectana* in Roewer (1942: 898). Blackwall's specimen was examined and found to be a large *Caerostris.* This agrees with a note left by D. J. Clark in 1960 with the vial. The specimen would be *C. vinsoni* Thorell according to the revision by Grasshoff (1984). This is a NEW SYNONYMY.

Separating Species. The pattern of the abdominal plates is the same in all species. The coloration is variable within species, perhaps preventing predators from acquiring a search image. All are about the same size, only *H. cryptocephala* being larger than others. We do not know whether or not the shape of the abdomen can be used to separate species. Only a few individuals were available of species that had the abdomen distinctly shaped. Thus, we do not know whether the anterior border of the abdomen of *H. tocantins* reflects variability of an individual or is characteristic of the species. The females are difficult to separate because the epigynum is simple and areas on its ventral face vary in sclerotization. Sometimes clues are provided by the posterior view or the internal placement of the seminal receptacles. The variation of the internal genitalia is not known, and they have not been used in the key.

To study the posterior face of the epigynum, make a slight cut with a mounted minutennadel to one side of the epigynum and a small cut anterior so the epigynum can be lifted. The epigynum, being lightly sclerotized, is easily damaged.

In contrast to females, males are easy to separate: many have diagnostic anterior projections from the carapace, and the median apophysis differs in different species, as does the complicated terminal apophysis, which for the most part is hid-

TABLE 1. SOME CHARACTERS BELONGING TO THE GENERA REVISED HERE AND *COLPHEPEIRA*, *GLYPTOGONA*, *MICRATHENA*, and *ASPIDOLASIUS*.

	HYP	ENC	XYL	GAS	MIC	ENA	GLY	COL	ASP*
Female									
Carapace square	–	+	–	+	–	–	–	–	+
Deep thoracic groove on carapace	–	–	–	–	[+]/–	–	–	–	–
Cephalic region as wide as thoracic	+	+	–/+	+	–	–	–	–	+
Cephalic region high	–	+	+	+	–	–	–	–	+
Thoracic region high	–	–	–	–	[+]/–	–	–	–	–
Clypeus high, more than 2× anterior median eyes	[1]	–	–	–	–	–	[2]	–	–
Sternum posterior, truncate or grooved	[1]	–	[2]	–	–	[3]	–	–	–
Femur 4 as long or longer than femur 1	+	+	+	+	[+]	+	–	–	–
Leg 4 longer than 1	–	+	+	+	[+]	–	–	–	–
Abdomen with sclerotized plates, spots	[1]	+	[2]	+	[3]	+	–	–	–
Abdomen shape	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]
Abdomen with median posterior tubercles	–	–	+	–	–	–	–	–	–
Stridulating ridges on book lungs	–	–	–	–	[+]/–	–	–	–	–
Sclerotized ring around spinnerets	–	–	+	+	+	+	–	–	–
Carapace with rim	–	–	–	–	[+]/–	–	–	–	–
Male									
Tarsal organ, P free, conical tibia	–	–	–	–	–	–	–	–	+
♂ Smaller than ♀, % of ♀ carapace width	77–95	37	25	25	28–86	75–94	106	100	30
Carapace square	–	–	–	–	–	–	–	–	+
Cephalic region almost as wide as thoracic	+	+	–/+	–	–	–	–	–	+
Cephalic region high	–	–	+	+	–	–	–	–	+
Lateral eyes on tip of projection	[+]	–	–	–	–	–	–	–	–
Median eye region projecting	–	–	–	[+]	–	–	–	–	–
Clypeus high, more than 2× anterior median eyes	[1]	–	–/+	–	–	–	[2]	–	–
Sternum	[1]	–	[2]	[3]	–	[4]	–	–	–
Femur 4 longer than femur 1	+	–	+	–	+	–	–	–	–
Leg 4 longer than leg 1	–	–	–	–	[+]	–	–	–	–
Endite tooth	–	–	–	–	–	+	+	+	–
Coxal hook	+	–	–	–	–/+†	+	+	+	–
Setae on palpal patella	1	1	1	1	1	1	1	1	1
Palpal bulb wider than long	–	+	+	–	–/+	–	–	–	–
Palpus with terminal apophysis	+	–	–	–	–/+	+	+	+	–
Palpus with paramedian apophysis	+?	+	+	+	+	+	–	–	–
Abdomen with sclerotized plate or spots	[1]	+	[2]	+	+	+	–	–	[3]
Abdomen shape specialized	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]
Sclerotized rings around spinnerets	–	–	+	+	+	+	–	–	–

* *Aspidolasius*, revised separately, is a tetragnathid.

† Coxal hook of male present when males are approximately more than 53% of size of females and absent when males are less than 53% of size of female, measured by percentage of width of carapace.

Genera. ASP, *Aspidolasius*; COL, *Colphepeira*; ENA, *Enacrosoma*; ENC, *Encyosaccus*; GAS, *Gasteracantha*; GLY, *Glyptogona*; HYP, *Hypognatha*; MIC, *Micrathena*; XYL, *Xylethrus*.

Codes. +, present; –, absent; –/+, absent, present in some species; [ ], an autapomorphy of genus.

Map 1. Distribution of *Hypognatha* species.

den between cymbium, tegulum, and embolus (Fig. 16).

KEY TO FEMALES OF *HYPOGNATHA*

Females of *H. cacau, H. carpish, H. furcifera, H. jacaze, H. maria,* and *H. tingo* are unknown or have not been matched to males.

The key is based entirely on the structure of the epigynum.

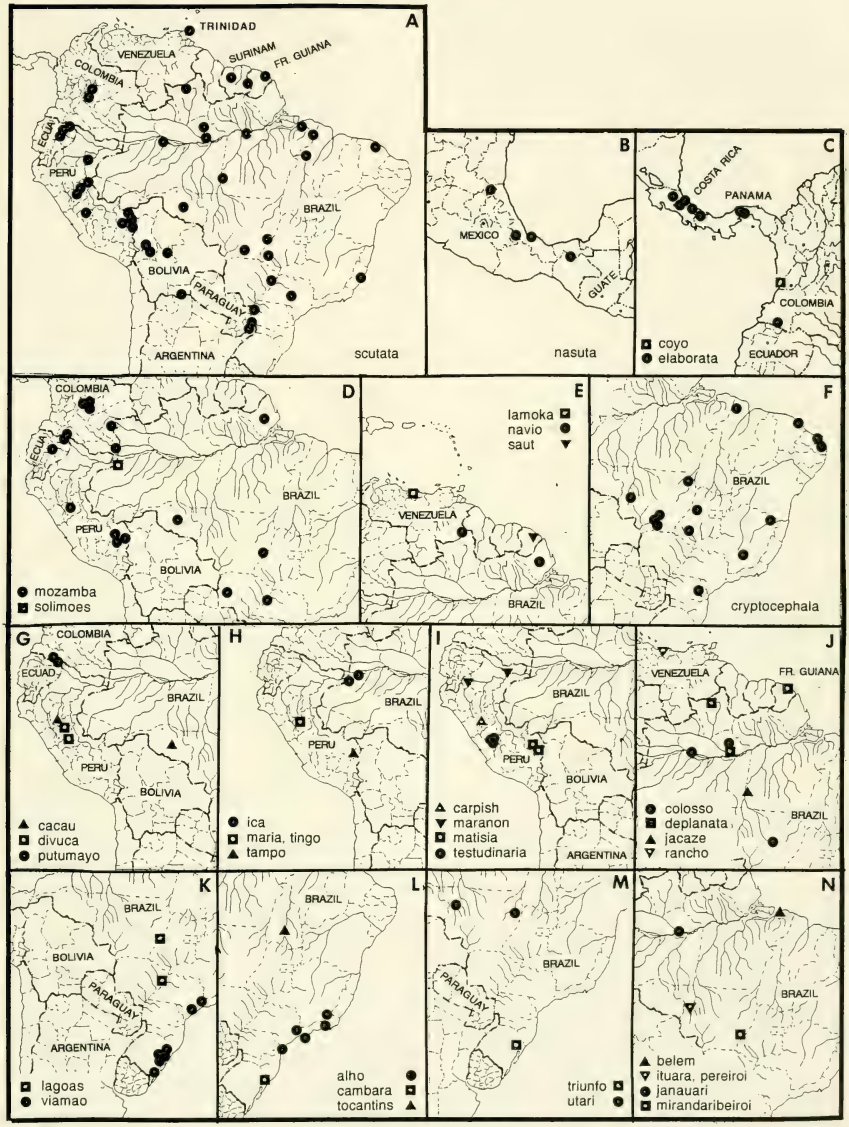
1. Ventral view of epigynum with the upper portion of two light circles visible at posterior margin (Figs. 56–58) ..... (in part) *scutata*
– Epigynum otherwise 2

2(1). Ventral view with a scape-like structure, as in Figure 67 ..... *navio*
– Epigynum otherwise 3

3(2). Posterior margin of epigynum has two margins, a transverse keel anterior and one posterior (Figs. 216, 217) ..... *colosso*
– Epigynum otherwise 4

4(3). Venter of epigynum with sclerotized sculpturing (Fig. 64) or a lightly sclerotized hump (Figs. 196, 200), neither of which is connected with the posterior margin 5
– All ventral sculpturing connected with posterior margin, or no sculpturing (Figs. 2, 24, 31, 56, 57, 77, 106) 6

5(4). Venter with small, median depression having a posterior lip (Fig. 64) ..... *saut*
– Venter with median hump (Figs. 196, 200) ..... *deplanata*
6(4). Ventral sculpturing connected to posterior margin (Figs. 2, 24, 31, 38, 45, 95) 7
– No ventral sculpturing except for lobes and notches of posterior margin, and sculpturing visible behind margin (Figs. 56, 77, 106, 112, 142, 154) 12
7(6). Venter with a transverse lip covering a median longitudinal line formed by adjacent lips or a depression (Figs. 2, 24, 31, 38, 45) 8
– Venter with longitudinal groove without lip (Fig. 95) ..... *mirandaribeiroi*
8(7). Posterior face with narrow, longitudinal, median plate (at 6 hr in Fig. 3) ..... *cryptocephala*
– Posterior face with median groove (Figs. 26, 33, 40, 46) 9
9(8). In posterior view parallel margins of lateral plates touching (Figs. 26, 33) 10
– In posterior view lateral plates, separated or touching only at small denticle lips (Figs. 40, 46, 97) 11
10(9). In ventral view width of anterior transverse edge about one-half length of visible longitudinal lips (Fig. 31) ..... *mozamba*
– In ventral view width of anterior transverse edge about two-thirds length of visible longitudinal lips (Fig. 24) .. *lagoas*
11(9). Epigynum as in Figures 45 and 46; Mexico ..... *nasuta*
– Epigynum as in Figures 38–40; Venezuela ..... *lamoka*
12(6). Ventral view of epigynum with shadows of two longitudinal bands, each bent on proximal end (Fig. 208), posterior with indistinct markings (Fig. 209) ..... *putumayo*
– Epigynum otherwise 13
13(12). Posterior margin with notches or lobes (Figs. 88, 106, 112, 128, 168, 208) 14
– Posterior margin straight or slightly curved without lobes or notches (Figs. 20, 56, 77, 142, 154, 162, 175) 18
14(13). Posterior margin with large notch (Fig. 128) ..... *pereiroi*
– Epigynum otherwise (Figs. 88, 106, 112, 168, 208) 15
15(14). Posterior margin with two indentations (Fig. 88) ..... *ituara*
– Posterior margin with lobes (Figs. 106, 112, 208) 16
16(15). Posterior lobe large, round, covered with tip of triangular sclerotized area (Fig. 112) ..... *cambara*
– Epigynum otherwise (Figs. 106, 168, 208) 17
17(16). Posterior face of epigynum with pair of dark circles separated by less than their diameter (Fig. 107) ..... *viamao*
– Posterior face with three round to cornered light areas, equal in diameter (Fig. 169) ..... *triunfo*
18(13). In ventral view of posterior margin, two distinct light circles touch margin from posterior (Figs. 56–58) .. (in part) *scutata*
– Epigynum otherwise 19
19(18). Posterior margin slightly concave, with a pair of lobes pressing against each other posteriorly (Figs. 20, 21) ..... *tampo*
– Epigynum otherwise 20
20(19). Posterior face with a pair of coiled margins (Figs. 143, 166, 184) 21
– Epigynum otherwise 23
21(20). Coils ventral (Fig. 143) ..... *elaborata*
– Coils dorsal (Figs. 166, 184) 22
22(21). Coils in a triangular light area (Fig. 184) ..... *divuca*
– Coils in a transverse rounded light area (Fig. 166) ..... *maranon*
23(20). Posterior face with circular, light, often indistinct, disks (Figs. 120, 136, 155, 172, 191, 194) 28
– Posterior face otherwise (Figs. 78, 132, 163, 176, 209, 230) 24
24(23). Posterior face of epigynum concave (Fig. 176) ..... *alho*
– Epigynum otherwise (Figs. 78, 132, 163, 209, 230) 25
25(24). Posterior face with sclerotized, tranverse shield (Fig. 132) ..... *belem*
– Posterior face otherwise (Figs. 78, 163, 230) 26
26(25). Posterior face with shadows of coils dorsally (Fig. 163) ..... *coyo*
– Posterior face otherwise (Figs. 78, 230) 27
27(26). Epigynum posterior face with light trapezoid area containing shadows of upside-down Js (Fig. 230) ..... *tocantins*
– Posterior view of epigynum with median light area widening near ventral margin (Fig. 78) ..... *testudinaria*
28(23). Posterior face with a pair of scales (Fig. 191), anterior with shadows of two parallel, longitudinal bands (Fig. 190) ..... *rancho*
– Epigynum otherwise 29
29(28). Ventral view with a sclerotized shield and two lateral, projecting bands (Fig. 171); posterior with two circles separated by slightly less than their diameter (Fig. 172) ..... *utari*
– Epigynum otherwise 30
30(29). Posterior face with light disks within wide frames (Figs. 120, 136) 31



Map 2. Distribution of *Hypognatha* species.

– Epigynum otherwise (Figs. 155, 194) 32
31(30). Venter of epigynum with sclerotized triangular area (Fig. 119) ..... *matisia*
– Venter as in Figure 134, posterior as in Figure 136 ..... *janauari*
32(30). In posterior view, with light disks touching (Fig. 194) ..... *solimoes*
– In posterior view, light disks separated (Fig. 155) ..... *ica*

KEY TO MALES OF *HYPOGNATHA*

Males of *H. alho, H. belem, H. coyo, H. ituara, H. janauari, H. maranon, H. mirandaribeiroi, H. pereiroi, H. rancho, H. saut, H. solimoes, H. tampo, H. tocantins, H. triunfo,* and *H. utari* are unknown.

1. Clypeus with median projection (Figs. 48, 49, 54, 123–125) 13
– Clypeus without median projection, sometimes with other median sculpturing (Figs. 6–8, 61, 92) 2
2(1). Lateral eyes, as seen in subdorsal view, on a projection longer than wide (Figs. 29, 86, 93, 101, 104) 8
– Lateral eyes on a wider than long or as wide as long projection (Figs. 7, 43, 62, 75, 110, 116) 3
3(2). Median area of clypeus with sculpturing (Figs. 42, 61, 109, 115) 4
– Median area of clypeus without sculpturing (Figs. 6, 73) 7
4(3). Clypeus with median transverse groove (Figs. 42, 61) 5
– Clypeus without such groove (Figs. 109, 115) 6
5(4). Venter of clypeus with a median bulge (Fig. 42) ..... *lamoka*
– Venter of clypeus with a median depression (Fig. 61) ..... *scutata*
6(4). Median apophysis with an "upper", small, sharp tooth (Fig. 111) ..... *viamao*
– Median apophysis forming a transverse gutter (Fig. 118) ..... *cambara*
7(3). Distal end of palpus with a projecting terminal apophysis (at 12 hr in Fig. 9) ..... *cryptocephala*
– Distal end of palpus with terminal apophysis forming a coil (at 11 hr in Fig. 76) ..... *navio*
8(2). Median area of clypeus with sculpturing (Figs. 28, 35, 92) 9
– Median area of clypeus plain (Figs. 85, 100, 103) 11
9(8). Clypeus with median dorsoventral ridge (Figs. 28, 35) 10
– Clypeus with small, median, distally divided tubercle (Fig. 92) ..... *carpish*
10(9). Terminal apophysis of palpus with a tooth (at 12 hr in Fig. 37) ..... *mozamba*
– Terminal apophysis of palpus without tooth (at 12 hr in Fig. 30) ..... *lagoas*
11(8). Median apophysis with three large prongs (at 4 hr in Fig. 105) ..... *maria*
– Median apophysis otherwise (Figs. 87, 102) 12
12(11). Median apophysis extends toward distal end of palpus, terminal apophysis a truncate, flat projection (Fig. 102) *tingo*
– Median apophysis extends toward lateral, proximal end of palpus; terminal apophysis with pointed projection (Fig. 87) ..... *testudinaria*
13(1). Tip of median clypeal projection pointed (Figs. 49, 180) 14
– Tip of median clypeal projection truncate or biforked (Figs. 124, 147, 158, 187, 204) 15
14(13). Median apophysis relatively small, distally pointed (Figs. 50, 51); Mexico ..... *nasuta*
– Median apophysis long, projecting, bent at a right angle (Figs. 181, 182) .... *cacau*
15(13). Median apophysis short, sclerotized (Figs. 150, 151, 160) 16
– Median apophysis long, soft, extended (Figs. 126, 188, 206, 214, 223, 228, 235) 17
16(15). Terminal apophysis a thick coil (at 12 hr in Figs. 150, 151) ..... *elaborata*
– Terminal apophysis otherwise, median apophysis with one forward, one reverse hook (Fig. 160) ..... *ica*
17(15). In mesal view median apophysis triangular, pointed (Figs. 127, 189) 18
– Median apophysis otherwise in mesal view (Figs. 207, 215, 224, 227, 236) .. 19
18(17). Two spines of median apophysis close to each other (Fig. 127) ..... *matisia*
– Two spines of median apophysis widely separated (Fig. 189) ..... *divuca*
19(18). Sickle-shaped terminal apophysis within loop of embolus (Fig. 228); median apophysis with four bulges (M in Fig. 227) ..... *furcifera*
– Terminal apophysis not sickle-shaped, or sickle-shaped structure above base of embolus (Figs. 206, 214, 223, 235); median apophysis with two or three bulges (Figs. 207, 215, 224, 236) 20
20(19). Terminal apophysis sickle-shaped, above base of embolus (Figs. 206, 214, 223) 21
– Terminal apophysis not sickle-shaped, above base of embolus (Fig. 235) *jacaze*
21(20). Median apophysis with three bulges (Figs. 206, 207) ..... *deplanata*
– Median apophysis otherwise (Figs. 215, 223) 22
22(21). Median apophysis as in Figures 214 and 215 ..... *putumayo*
– Median apophysis as in Figures 223 and 224 ..... *colosso*

Hypognatha cryptocephala Mello-Leitão
Figures 2–16; Map 2F

Hypognatha cryptocephala Mello-Leitão, 1947: 246, fig. 12, ♀. Female holotype from Vila Velha, Ponta Grossa [Paraná State, Brazil], in MNHC, examined. Brignoli, 1983: 271.

Note. The female holotype is shrivelled and was wrapped in fungal mycelium. The abdomen was carefully cleaned using an ultrasonic vibrator and needles. The specimen had a label, "*H. coccinelloides*". The epigynum has a posterior, median plate shaped as in other specimens, but the ventral lip (facing posteriorly) is slightly more curved medially than in the illustration (Fig. 3). The measurements of this, the largest *Hypognatha* species, are almost the same as those in the description by Mello-Leitão.

Description. Female from Cuiabó, Mato Grosso, Brazil. Carapace, chelicerae, endites, sternum orange-brown. Coxae, legs reddish brown; distal articles of legs orange. Abdomen reddish brown with pairs of white patches (Fig. 5); venter black. Chelicerae with six anterior teeth. Total length 4.8 mm. Carapace 2.3 mm long, 2.0 wide in thoracic region, 2.1 wide in cephalic region. First femur 1.2 mm, patella and tibia 1.5, metatarsus 1.1, tarsus 0.5. Second patella and tibia 1.4 mm, third 1.1. Fourth femur 1.5 mm, patella and tibia 1.5, metatarsus 1.0, tarsus 0.5. Abdomen 4.5 mm long, 4.8 wide.

Male from Cuiabó, Mato Grosso, Brazil. Coloration as in female. Venter of first two femora with short macrosetae, three on first, two on second. Abdomen as in female. Total length 4.5 mm. Carapace 2.1 mm long, 1.8 wide in thoracic region, 1.8 wide in cephalic region. First femur 1.2 mm, patella and tibia 1.6, metatarsus 1.2, tarsus 0.6. Second patella and tibia 1.4 mm, third 1.0. Fourth femur 1.3 mm, patella and tibia 1.3, metatarsus 1.0, tarsus 0.5. Abdomen 3.4 mm long, 3.4 wide.

Note. Males and females were collected together.

Variation. Total length of females 4.0 to 6.0 mm, males 3.2 to 3.8. The illustrations (Figs. 2, 3, 5) of the female were of a specimen from Minas Gerais, Figure 4 of a female from Santo Antonio, the male from specimens from Mato Grosso.

Diagnosis. The female is larger than females of any other species and the epigynum, in posterior view, has a distinct, narrow, median plate (Fig. 3). The male palpus, unlike others, has a distal projection, a part of a sclerite between embolus and terminal apophysis (Fig. 9, A in Figs. 12, 13).

Specimens Examined. BRAZIL *Maranhão:* Aldeia Maracaçumé, Rio Maracaçumé, 80 km E Canindé, 22, 23 May 1963, 1♀ (B. Malkin, AMNH). *Ceará:* Fortaleza, June-Sept. 1911, 9♀ (W. M. Mann, MCZ). *Rio Grande do Norte:* Fazenda Canaã [05°57′S, 35°26′W], 24 Feb. 1952, 3♀, 7♂ (M. Alvarenga, MZSP 7970). *Paraíba:* Independencia [Guarabira], 1911, 2♀, 8 imm. (W. M. Mann, MCZ). *Goiás:* Aceiro, Jataí, Oct. 1962, 4♀, 1♂ (Exped. Mus. Zool., MZSP 3091, 4191, 4192, 8329), Dec. 1963, 1♀ (M. Alvarenga, AMNH); Goiás, 4♀ (MNHN 21621). *Mato Grosso:* Barra do Tapirapé, 5–23 Nov. 1964, 1♀ (B. Malkin, AMNH); Chapada dos Guimarães, Nov. 1963, 3♀ (M. Alvarenga, AMNH); Cuiabá, Nov. 1963, 2♀, 1♂ (M. Alvarenga, AMNH); Santo Antônio de Leverger, 6 Oct. 1981, 12♀, 11♂ (M. I. Maeques, MCP 2525); Utiariti, Oct. 1966, 1♀ (Lanko, P. F. S. Pereiro, MZSP 5608). *Minas Gerais:* Lagoa Santa, 1♂ (Reinhardt, ZMUC); Pedra Azul, Dec. 1970, 2♀ (P. M. Oliveira, AMNH).

Hypognatha tampo new species
Figures 20–23; Map 2H

Holotype. Female holotype from Zona Reservada Tambopata, 290 m, Depto. Madre de Dios, 12°50′S, 69°17′W, Peru, 11 May to 12 June 1988 (D. Silva D.), in MUSM. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace dark orange, sides of thoracic region dusky. Chelicerae, endites, sternum, dark orange, with sternum dusky. Legs light orange. Abdomen orange underlaid by white pigment spots, with venter gray. Total length 3.2 mm. Carapace 1.43 mm long, 1.15 wide in thoracic region, 1.14 wide in cephalic region. First femur 0.91 mm, patella and tibia 0.92, metatarsus 0.68, tarsus 0.40. Second patella and tibia 0.92 mm,

third 0.62, fourth 0.89. Fourth femur 0.91 mm. Abdomen 2.6 mm long, 2.9 wide.

Diagnosis. In *H. tampo,* lateral and posterior margins of the transverse depression are sclerotized (Figs. 21, 22), whereas in *H. lagoas* and *H. mozamba* the anterior and lateral margins are sclerotized (Figs. 24, 25, 31, 32). Also, *H. tampo* has the posterior median slit shorter (Fig. 22) than in the other two species (Figs. 26, 33), and the internal genitalia appear to be two areas about as wide as long (Fig. 23), whereas the two other species have cone-shaped internal genitalia (Figs. 27, 34).

Specimens Examined. No other specimens were found.

Hypognatha lagoas new species
Figures 24–30; Map 2K

Holotype. Male holotype from Três Lagoas, Mato Grosso do Sul, Brazil, 16 Sept. 1964 (Exped. Dept. Zool.), in MZSP no. 3651. The specific name is a noun in apposition after the locality.

Description. Female from Chavantina. Carapace, chelicerae, endites, sternum, orange. Legs light orange. Abdomen dorsum white with light orange plates, venter light gray. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Total length 2.7 mm. Carapace 1.46 mm long, 1.15 wide in thoracic region, 1.18 wide in cephalic region. First femur 0.92 mm, patella and tibia 1.03, metatarsus 0.67, tarsus 0.44. Second patella and tibia 0.96 mm, third 0.65, fourth 0.92. Fourth femur 0.95 mm. Abdomen 2.8 mm long, 2.7 wide.

Male holotype. Coloration as in female. Second tibia with four, short, ventral macrosetae. Total length 2.5 mm. Carapace 1.30 mm long, 1.08 wide in thoracic region, 1.04 wide in cephalic region. First femur 0.89 mm, patella and tibia 1.03, metatarsus 0.81, tarsus 0.43. Second patella and tibia 0.93 mm, third 0.61, fourth 0.87. Fourth femur 0.87 mm. Abdomen 2.0 mm long, 2.0 wide.

Note. The match of males and females is uncertain. They were placed together because of their similarities to *H. mozamba.*

Variation. Total length of females 2.7 to 3.4 mm. The female in the MZSP had the abdomen wider than long and had a median tubercle in the center of median and lateral plates. The illustrations were from the holotype and the female described.

Diagnosis. In *H. lagoas* the anterior transverse lip is larger and closer to the posterior margin of the epigynum (Fig. 24) than in *H. mozamba* (Fig. 31). The male clypeus of *H. lagoas* has two depressions, perhaps to hold the female fang when mating (Fig. 28); these depressions are absent in *H. mozamba* (Fig. 35). The terminal apophysis of the palpus (Fig. 30) differs from that of *H. mozamba* by lacking the distal tooth present in the palpus of *H. mozamba* (at 12 hr in Fig. 37).

Specimens Examined. BRAZIL *Mato Grosso:* Chavantina, July 1946, 1♀ (H. Sick, MZSP 8047), June 1947, 1♀ (G. Carvalho, MNRJ).

Hypognatha mozamba new species
Figures 1, 31–37, 52, 53; Map 2D

Holotype. Male holotype, one female and two male paratypes from Hacienda Mozambique, 500 m, 15 km SW Puerto Lopez, Depto. Meta, Colombia, no date (W. Eberhard), in MCZ. The specific name is an arbitrary combination of letters.

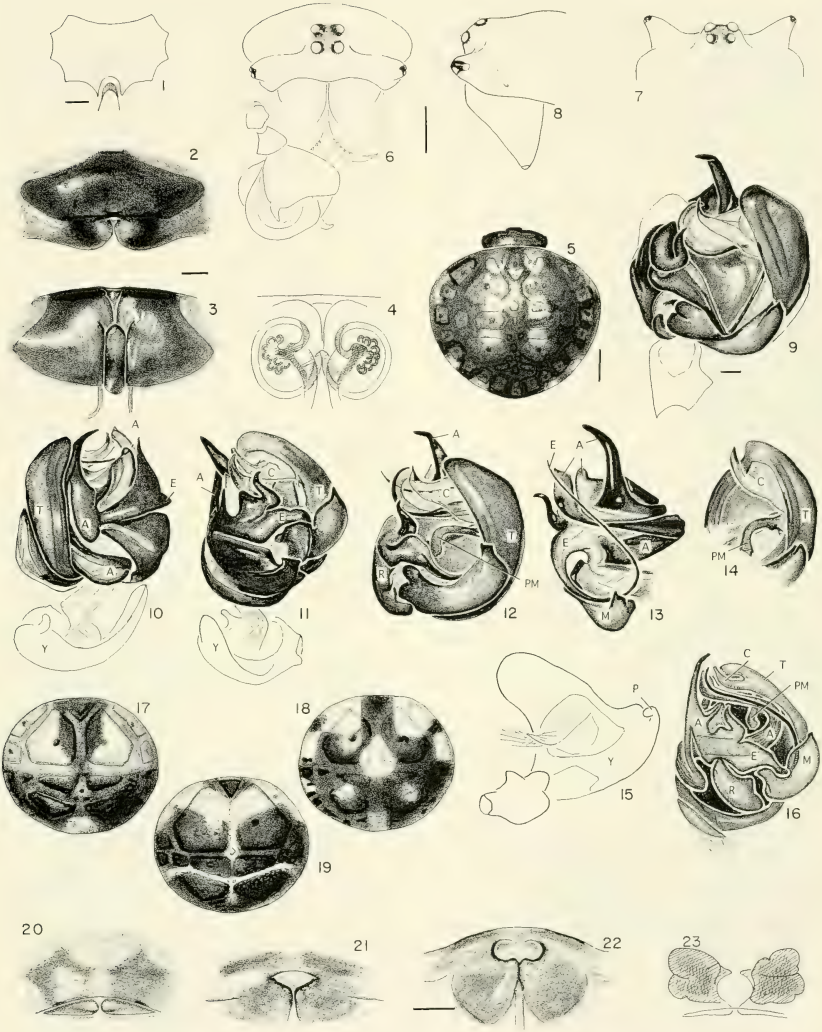
Hypophthalma sp., Eberhard, 1986: 73.

Description. Female paratype. Carapace, chelicerae, sternum orange. Coxae, legs light orange. Abdomen orange with white pigment spots; venter orange-gray. Abdomen with central, dorsal hump (Fig.

→

Figure 1. Sternum of *Hypognatha mozamba.*

Figures 2–16. *H. cryptocephala* Mello-Leitão. 2–5, female. 2–4, epigynum. 2, ventral. 3, posterior. 4, cleared. 5, dorsal. 6–16, male. 6, eye region, chelicerae and right palpus. 7, eye and chelicera, subdorsal. 8, eye region, lateral. 9–16, left male palpus. 10–16, palpus pulled apart. 10, mesal. 11, mesoventral. 12, ventral. 13, bulb, dorsal. 14, ventral showing conductor and paramedian apophysis. 15, cymbium. 16, ventral, diagrammatic.



Figures 17–19. Dorsal pattern of abdomen of three immature *H. colosso* collected together.

Figures 20–23. *H. tampo* n. sp., epigynum. 20, ventral. 21, ventroposterior. 22, posterior. 23, cleared.

Abbreviations. A. terminal apophysis. C, conductor. E, embolus. M, median apophysis. P, paracymbium. PM, paramedian apophysis. R, radix. T, tegulum. Y, cymbium.

Scale lines. 1.0 mm; Figure 1 and genitalia 0.1 mm; eye regions 0.5 mm.

52). Total length 3.8 mm. Carapace 1.60 mm long, 1.36 wide in thoracic region, 1.35 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.15, metatarsus 0.78, tarsus 0.44. Second patella and tibia 1.08 mm, third 0.84, fourth 1.05. Fourth femur 1.06 mm. Abdomen 2.9 mm long, 3.1 wide.

Male holotype. Coloration as in female. Sternum as wide as long. No macrosetae on second femur. Abdomen as in female. Total length 2.5 mm. Carapace 1.40 mm long, 1.07 wide in thoracic region, 1.04 wide in cephalic region. First femur 0.84 mm, patella and tibia 1.13, metatarsus 0.90, tarsus 0.42. Second patella and tibia 0.99 mm, third 0.65, fourth 0.90. Fourth femur 0.87 mm. Abdomen 2.1 mm long, 2.1 wide.

Note. Males and females were easily matched, as numerous males and females were collected together.

Variation. Total length of females 2.8 to 4.2 mm, males 2.1 to 2.8. The illustrations were made from the holotype and paratypes.

Diagnosis. The female can be separated from that of *H. lagoas* by having the median slit of the epigynum (Fig. 31) more than twice the width of the anterior depression in *H. mozamba,* less than twice in *H. lagoas* (Fig. 24). The male palpus in *H. mozamba* differs by having a tooth on the terminal apophysis (at 12 hr in Fig. 37), absent in *H. lagoas* (Fig. 30).

Natural History. The species has been collected in rainforest in Rondônia. The web was illustrated by Eberhard (1986: 73, fig. 4.2e).

Paratypes. COLOMBIA *Meta:* Hacienda Mozambique, 15 km SW Puerto Lopez, 200 m, no date, 2♀, 3♂ (W. Eberhard 1499, MCZ), July 1978, 2♀, 2♂ (W. Eberhard 1619, 1714, MCZ); Aug. 1978, 1♀ (W. Eberhard, MCZ).

Specimens Examined. COLOMBIA *Meta:* Lomalinda, 300 m, Puerto Lleras, 3°16′N, 73°23′W, 10 Nov. 1985, 1♀ (B. Carroll, MCZ), May 1987, 1♀; June 1987, 1♀; Aug. 1988, 1♀ (all B. Carroll, CAS), Mar. 1987, 1♀ (V., B. Roth, CAS); Villavicensio, 24 July 1938, 1♀ (H. Dybas, MCZ). *Vaupés:* Mitú, 200 m, Feb. 1975, 1♀ (P. A. Schneble, MCZ). *Putumayo:* Buena Vista, 0°25′N, 76°25′W, 23–29 July 1972, 2♀ (W. Eberhard, MCZ). *Amazonas:* Río Pira, Río Apaporis, 0°25′S, 70°15′W, 7–15 Feb. 1989, 1♀ (V., B. Roth, CAS). ECUADOR *Sucumbíos:* Limon Coda [Limoncocha], 10 Aug. 1965, 1♀ (C. B. Patrick, MCZ); Río Tarpoy., 28 Apr. 1989, 1♀ (L. Aviles, MECN); Río Tarapuy, junction road from Tarapoa, 24 June 1988, 4♀, 5♂ (W. Maddison, MCZ); Tarapoa, 0°07′S, 76°20′W, 5♀ (W. Maddison, MCZ); bridge over Río Cuyabeno, 00°18′S, 76°18′W, 25–30 June 1988, 3♀ (W. Maddison, MCZ). *Napo-Pastaza:* Huagra-Yacu, "Oriente" (Brown, 1941), Apr. 1941, 1♀ (W. Clarke-Macintyre, AMNH). *Pastaza:* Puyo, 18 Apr. 1958, 4♀ (R. W. Hodges, MCZ); 4.5 km N Puyo, 953 m, 9 Feb. 1955, 1♀, 1 imm. (E. I. Schlinger, E. S. Ross, CAS). PERU *Huánuco:* El Castillo, Tingo María, 2 June 1967, 2♀ (A. F. Archer, S. Ricco, AMNH); Tingo María, 1♀ (J. C. Pallister, AMNH), Oct. 1946, 1♀, 1♂, Dec. 1946, 1♀ (both W. Weyrauch, AMNH). *Cuzco:* Quincemil, 720 m, 24–27 Apr. 1947, 1♀ (J. C. Pallister, AMNH). *Madre de Dios:* Zona Reservada de Manu, Pueste de Control Pakitza, 11°58′S, 71°18′W, 25 Sept. 1987, 1♂ (J. Coddington, D. Silva D., USNM); Zona Reservada Pakitza, 11°58′S, 71°18′W, 26 Sept. 1987, 1♀ (J. Coddington, D. Silva D., MUSM); Tambopata Reserve, Río Tambopata, 30 Mar. 1988, 1♀ (J. Palmer, D. Smith, MCZ); Río Alto Madre de Dios, Playa Maronal, 24 Oct. 1987, 1♀ (D. Silva D., MUSM). BRAZIL *Amapa:* Serra do Navio, July 1966, 1♀ (M. E. Galiano, MACN). *Rondônia:* Fazenda Rancho Grande nr. Cacaulandia, 6–15 Dec. 1990, 3♀, 1♂ (G. B. Edwards, FSCA). *Mato Grosso:* Chavantina, Dec. 1946, 1♀ (H. Sick, MZSP 8047), June 1947, 1♀, 1 imm. (J. G. Carvalho, MNRJ). *Mato Grosso do Sul:* Pousada Caiman, Miranda, 6 May 1991, 1♀ (A. C. Meyer, MCN 21002). *São Paulo:* Lussanvira, 1♀ (R. Arlé, MNRJ).

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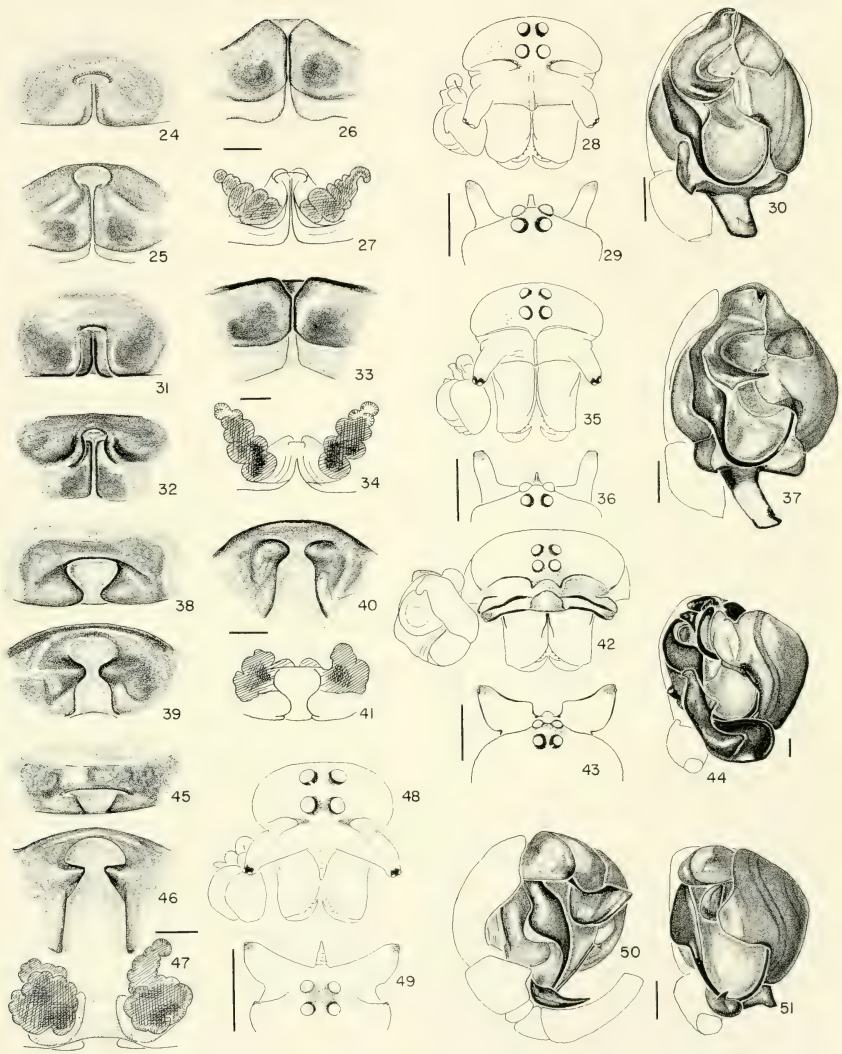
Figures 24–30. *Hypognatha lagoas* n. sp. 24–27, epigynum. 24, ventral. 25, ventroposterior. 26, posterior. 27, cleared. 28–30, male. 28, eye region, chelicerae and right palpus. 29, eye region, subdorsal. 30, left palpus.

Figures 31–37. *H. mozamba* n. sp. 31–34, epigynum. 31, ventral. 32, ventroposterior. 33, posterior. 34, cleared. 35–37, male. 35, eye region, chelicerae and right palpus. 36, eye region, subdorsal. 37, palpus.

Figures 38–44. *H. lamoka* n. sp. 38–41, epigynum. 38, ventral. 39, ventroposterior. 40, posterior. 41, cleared. 42–44, male. 42, eye region, chelicerae and right palpus. 43, eye region, subdorsal. 44, palpus.



Figures 45–51. *H. nasuta* O. P.-Cambridge. 45–47, epigynum. 45, ventral. 46, posterior. 47, cleared. 48–51, male. 48, eye region, chelicerae and right palpus. 49, eye region, subdorsal. 50, palpus, mesal. 51, palpus, ventral.

Scale lines. Eye regions 0.5 mm; genitalia 0.1 mm.

Hypognatha lamoka new species
Figures 38–44; Map 2E

Holotype. Male holotype from La Moka, Caracas, Venezuela, 5–7 Aug. 1891 (Meinert), in ZMUC. The specific name is a noun in apposition after the locality. La Moka is assumed to be the name of a house.

Description. Female paratype. Carapace, chelicerae, endites, sternum orange-brown. Legs orange-brown, coxae orange. Abdomen dark, orange-brown, spaces between plates darker than plates; venter lighter gray. Total length 4.0 mm. Carapace 1.42 mm long, 1.26 wide in thoracic region, 1.29 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.11, metatarsus 0.80, tarsus 0.44. Second patella and tibia 1.09 mm, third 0.73, fourth 0.97. Fourth femur 1.08 mm. Abdomen 3.2 mm long, 3.5 wide.

Male holotype. Lighter than female in color, dorsum of abdomen with some white anteriorly, dusky posteriorly. Second tibia thicker than first and slightly twisted, ventrally with indistinct, tiny macrosetae. Total length 2.9 mm. Carapace 1.19 mm long, 1.17 wide in thoracic region, 1.14 wide in cephalic region. First femur 0.91 mm, patella and tibia 1.05, metatarsus 0.79, tarsus 0.40. Second patella and tibia 0.93 mm, third 0.63, fourth 0.85. Fourth femur 0.99 mm.

Note. Males and females were collected at the same location.

Variation. Total length of females 3.1 to 4.0 mm.

Diagnosis. In *H. lamoka,* the depression of the epigynum (Fig. 38) is larger than in *H. lagoas* (Fig. 24), and the posterior view of the epigynum (Fig. 40) shows the rim of the anterior depression less distinctly than in *H. nasuta* (Fig. 46). The male of *H. lamoka* (Fig. 43) lacks the median projection of the carapace of *H. nasuta* (Fig. 49), and its palpus has a larger median apophysis (at 6 hr in Fig. 44) than that of *H. nasuta* (Fig. 51).

Paratypes. VENEZUELA *Distrito Federal:* Caracas, 4–25 July 1891, 1♀; Río Catuche, Caracas, 9–21 July 1891, 1♀; La Moka, Caracas, Aug. 1891, 1♀ (all Meinert, ZMUC, one in MCZ).

Specimens Examined. VENEZUELA *Distrito Federal:* Caracas, 1♀ (V. Ben Khien, MNRJ).

Hypognatha nasuta
O. P.-Cambridge
Figures 45–51, 54, 55; Map 2B

Hypognatha nasuta O. P.-Cambridge, 1896: 222, pl. 27, figs. 3–5, ♀, ♂. Two female and one male syntypes from Teapa, Tabasco, Mexico, in BMNH no. 1905.4.28.3487–3496(part), examined. F. P.-Cambridge, 1904: 540, pl. 51, figs. 27, 28, ♀, ♂. Roewer, 1942: 894. Chickering, 1953: 6, figs. 11–15, ♀, ♂. Bonnet, 1957: 2258.

Description. Female from Veracruz State, Mexico. Carapace orange, lightest posteriorly. Chelicerae, endites, labium orange. Sternum dusky orange. Legs orange. Abdomen orange, with venter lighter than dorsum, some gray in middle of venter. Total length 3.7 mm. Carapace 1.58 mm long, 1.23 wide in thoracic region, 1.27 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.14, metatarsus 0.83, tarsus 0.48. Second patella and tibia 1.08 mm, third 0.72, fourth 1.04. Fourth femur 1.1 mm. Abdomen 3.4 mm long, 3.5 wide.

Male holotype. Coloration as in female. Five minute macrosetae on right second tibia, two on left. Total length 2.5 mm. Carapace 1.18 mm long, 1.00 wide in thoracic region, 0.92 wide in cephalic region. First femur 0.83 mm, patella and tibia 1.02, metatarsus 0.70, tarsus 0.39. Second patella and tibia 0.92 mm, third 0.58, fourth 0.78. Fourth femur 0.79 mm (specimen from near La Palma). Abdomen 2.0 mm long, 2.0 wide.

Note. Males and females were collected together.

Variation. Total length of males 2.2 to 2.5. The illustrations were made from Veracruz State specimens.

Diagnosis. The female *H. nasuta* differs by having the anterior depression of the epigynum more distinct in posterior view (Fig. 46) than that of *H. lamoka* (Fig. 40). The male *H. nasuta* has a distinct, median, pointed annulate extension on the clypeus

(Fig. 49), absent from all other *Hypognatha* (Fig. 43).

Natural History. O. P. Cambridge (1896) reported in a note with the description that it had been found on open, wet ground, near a highland stream, in a coarse, slanting orb, 12 to 15 cm diameter, about 2.5 m above ground, supported by lines 1.5 m long, among trees 3 m apart, with the spider in the hub.

Specimens Examined. MEXICO *San Luis Potosí:* Tamanzuchale, 18–20 July 1946, 1♂ (J. C., D. L. Pallister, AMNH). *Veracruz:* Cordoba, 14 May 1946, 1♀ (J. C., D. L. Pallister, AMNH); Estación de Biología Tropical "Los Tuxtlas", nr. La Palma, 18°36′N, 95°07′W, 29 June–1 July 1983, 1♂ (W. Maddison, MCZ).

Hypognatha scutata (Perty) Figures 56–63; Map 2A

Acrosoma scutatum Perty, 1833: 194, pl. 38, fig. 7. Specimens from Provincia Bahiensis, in ZSM, destroyed during the Second World War.

Gasteracantha Feisthameli Guérin-Méneville, 1840: 110. Specimen from Cayenne, French Guyana, in MNHN, not examined. First synonymized by Simon, 1895b: 871.

Eurysoma scutatum:—C. L. Koch, 1839: 117, fig. 517, ♀. Keyserling, 1880: 293, pl. 4, fig.1, ♀, ♂.

? *Micrathena squammosa* Simon, 1864: 293. Immature holotype, total length 1.5 mm, from Brazil, in MNHN, examined. Doubtful NEW SYNONYMY.

Calydna prospiciens O. P.-Cambridge, 1874: 175, fig. 3, ♂. Male holotype from Minas Gerais, Brazil (H. Rogers), in HECO, examined. First placed in *Hypognatha* by Simon, 1895b. NEW SYNONYMY.

Paraplectana decora O. P.-Cambridge, 1877: 34, pl. 7, fig. 8, ♀. Female holotype from "Rio Grande, South America" (H. Rogers) [on a copy of holotype label: S. Brazil], in HECO, B 1160, examined. NEW SYNONYMY.

Hypophthalma coccinellina Taczanowski, 1879: 125, pl. 2, fig. 37, ♀. One female, 3 imm. syntypes from Amable María [Tarma Prov., Junín], Peru, in PAN, examined. NEW SYNONYMY.

Paraplectana scutata:—Keyserling, 1892: 2, pl. 1, fig. 2, ♀, ♂.

Hypognatha scutata:—Simon, 1895b: 871, 874, figs. 932–935, ♀, ♂. Roewer, 1942: 894. Bonnet, 1957: 2258.

Hypognatha squammosa:—Simon, 1895b: 874. Roewer, 1942: 894.

Hypognatha prospiciens:—Simon, 1895b: 872. Roewer, 1942: 893. Bonnet, 1957: 2258.

Hypognatha decora:—Simon, 1895b: 874. Roewer, 1942: 894. Bonnet, 1957: 2258.

? *Hypognatha cruciata* Tullgren, 1905: 36, pl. 5, fig. 13, imm. Immature holotype from Tatarenda, Chaco [Tatarenda, Tarija, 600 m, 21°50′S, 63°37′W (Paynter, 1992)], Bolivia, in NRMS, examined. Roewer, 1942: 893. Bonnet, 1957: 2258. Doubtful NEW SYNONYMY.

Hypognatha coccinellina:—Roewer, 1942: 893. Bonnet, 1957: 2258.

Hypognatha squamosa:—Bonnet, 1957: 2259.

Note. Neither Perty's description nor that of C. L. Koch is recognizable to species. The first time the name *scutata* was assigned to a species with adequate illustration was by Keyserling (1880, 1892). I am following Keyserling's use. Koch (1839) had examined Perty's specimen earlier in the Munich museum. Specimens from the BMNH, no. 15.3.5.1895.96, considered types of *Acrosoma scutata,* included a male and a female. Inside the vial was a 5-by-9-mm label with "Brasilien, E. Simon" in clear, clean handwriting and a larger, blue-bordered label, 20 by 26 mm, with a faint, large, barely visible "Eurysoma scutata Pert.". This specimen apparently moved from Paris to Keyserling and served for Keyserling's description of *Eurysoma scutata* (1880). Keyserling (1880, 1892) cited only three localities: Cayenne, Neu Granada [Colombia], and Peru. He does not mention the locality for either *A. scutatum* (Bahia State, Brazil), or the specimen illustrated and labeled by C. L. Koch (Brazil).

The vial with the original specimens of *C. prospiciens* was labeled as *Mutina prospiciens.* According to I. Lansbury (personal communication, 1994), O. P.-Cambridge usually listed all material in a bottle on a single large label referring to each tube with a number. Thus, the labels that come with loaned specimens are all copied from the label in the jar.

Micrathena squammosa Simon was spelled with one *m* by Bonnet (1957: 2259). The name *squamosa* may be preoccupied by *Plectana squamosa* Walckenaer (1836: 202) [=*Micrathena sexspinosa* (Hahn)]. *Plectana,* with the type species *cancriformis,* is a synonym of *Gasteracantha* but originally contained many *Micrathena* descriptions. It was not possible

to place the immature holotype, so it is here placed in the most common, widespread species of *Hypognatha*.

The holotype of *H. cruciata* is also immature (total length about 3 mm); it is placed here with the most common species, as its distribution fits that of *H. scutata* (Map 2A).

Description. Female from Trinidad. Carapace, chelicerae, sternum, legs reddish brown. Abdomen reddish brown with venter lighter than dorsum. Total length 4.0 mm. Carapace 1.7 mm long, 1.5 wide in thoracic region, 1.7 wide in cephalic region. First femur 1.0 mm, patella and tibia 1.2, metatarsus 0.8, tarsus 0.5. Second patella and tibia 1.1 mm, third 0.8, fourth 1.1. Fourth femur 1.1 mm. Abdomen 2.9 mm long, 3.3 wide.

Male from Trinidad. Coloration as in female. Second tibia gently curved. Abdomen as in female. Total length 2.7 mm. Carapace 1.82 mm long, 1.43 wide in thoracic region, 1.37 wide in cephalic region. First femur 1.10 mm, patella and tibia 1.32, metatarsus 1.01, tarsus 0.53. Second patella and tibia 1.31 mm, third 0.79, fourth 1.09. Fourth femur 2.0 mm. Abdomen 2.5 mm long, 2.9 mm wide.

Note. Males and females were collected together.

Variation. Some individuals have symmetrical pairs of white patches. Total length of females 3.1 to 5.7 mm, but most females less than 4 mm, males 2.5 to 3.6, most males less than 3 mm. All illustrations were made from specimens from Trinidad.

Diagnosis. The female is separated from others by having posteriorly, in subventral view of the epigynum, two adjacent, light, colored circles (Fig. 57, at 12 hr in Fig. 58). The male is separated from others by the sculpturing of the eye region (Fig. 61), the shape of the median apophysis (at 6 hr in Fig. 63), and the U-shaped portion of the terminal apophysis (at 11 hr in Fig. 63).

Natural History. Simon (1895a) wrote that the spider builds a regular orb web.

Specimens Examined. LESSER ANTILLES *Trinidad:* Arima, May 1953, 1♂ (N. L. H. Krauss, AMNH), 24–26 July 1978, 2♀ (D. A. Brady, AMNH); 6.4 km N Arima, 23 Aug. 1986, 1♀, 1 imm. (G. B. Edwards, FSCA); nr. Simla, 20–23 Aug. 1986, 3♀, 1♂, 1 imm. (G. B. Edwards, FSCA); Arima Valley, 10–22 Feb. 1964, 1♀, 1 imm. (J. Rozen, P. Wygodzinsky, AMNH); Simla, Arima Valley, Dec. 1954, 1♀, 2♂, 18 imm. (A. M. Nadler, AMNH), 23 Apr. 1964, 1♂ (A. M. Chickering, MCZ); 10 May 1981, 1♂, 2♀ (R. West, MCZ); Diego Martin, 9 Oct. 1944, 1♀ (R. H. Montgomery, AMNH), 23 Aug. 1963, 1♀ (E. N. K.-Waering, AMNH); Maracas Valley, 16 July, 1964, 1♀ (J. Lazell, MCZ); Mount Tucuche, April 1929, 5♀, 4♂, 2 imm. (P. J. Darlington, MCZ); Port of Spain, 1913, 19♀, 7♂, 58 imm., no date, 6♀, 6♂, 37 imm. (R. Thaxter, MCZ); Navy Base, SW Trinidad, Sept. 1944, 1♀, 1 imm.; Nov. 1944, 6♀ (R. Ingle, AMNH). SURINAM *Saramacca:* Voltzberg, 15 Dec. 1980, 1♀ (D. Smith, MCZ); Voltzberg-Raleighvallen Reserve, 4°45N, 56°10′W, 4♀, 5 imm. (D. Smith, MCZ). *Marowijne:* Anapaike village, Lawa River, 27–29 Nov. 1963, 1♀ (B. Malkin, AMNH). COLOMBIA *Meta:* Río Duda, Macarena, 450 m, 1992, 2♀ (R. Calixto, RC); 4.9 km W Villavicencio, 11 Mar. 1955, 3♀, 1♂, 14 imm. (E. I. Schlinger, E. S. Ross, CAS). ECUADOR *Sucumbíos:* Limoncocha, 24–26 June 1980, 1♀ (H. V., C. B. Weems, FSCA). *Napo:* 20 km E Puerto Napo, Alimahui, 01°00′S, 77°25′W, Aug. 1994, 1♀ (V. D. Roth, CAS); Coca, Río Napo, May 1965, 1♀ (L. Peña, MCZ); Yusupiijo, 520 m, 1°03′S, 72°48′W, 14 Aug. 1989, 1♀ (A. Bien, P. Ruby, MECN). PERU *Loreto:* Río Samiria, May 1990, 1♂ (D. Silva, MUSM). *Ucayali:* El Indio, Contamana, 8 Sept. 1986, 1♀ (P. Hocking, MUSM); 107 km E Tingo María, 16 Nov. 1954, 2♀ (E. I. Schlinger, E. S. Ross, CAS). *Junín:* Utcuyacu, Feb.–Apr. 1948, 15♀, 8♂, 25 imm. (F. Woytkowski, AMNH). *Madre de Dios:* Iberia, 30 Apr. 1947, 1♀ (J. C. Pallister, AMNH); Zona Reserva Tambopata, 48 km SW Puerto Maldonado, 12°50′S, 69°20′W, 1–4 May 1984, 1♀ (W. J. Pulawski, CAS); 12°50′S, 69°17′W, 16 Aug. 1986, 1♀ (I. Bohorquez, MUSM); 15 May 1988, 1♀,

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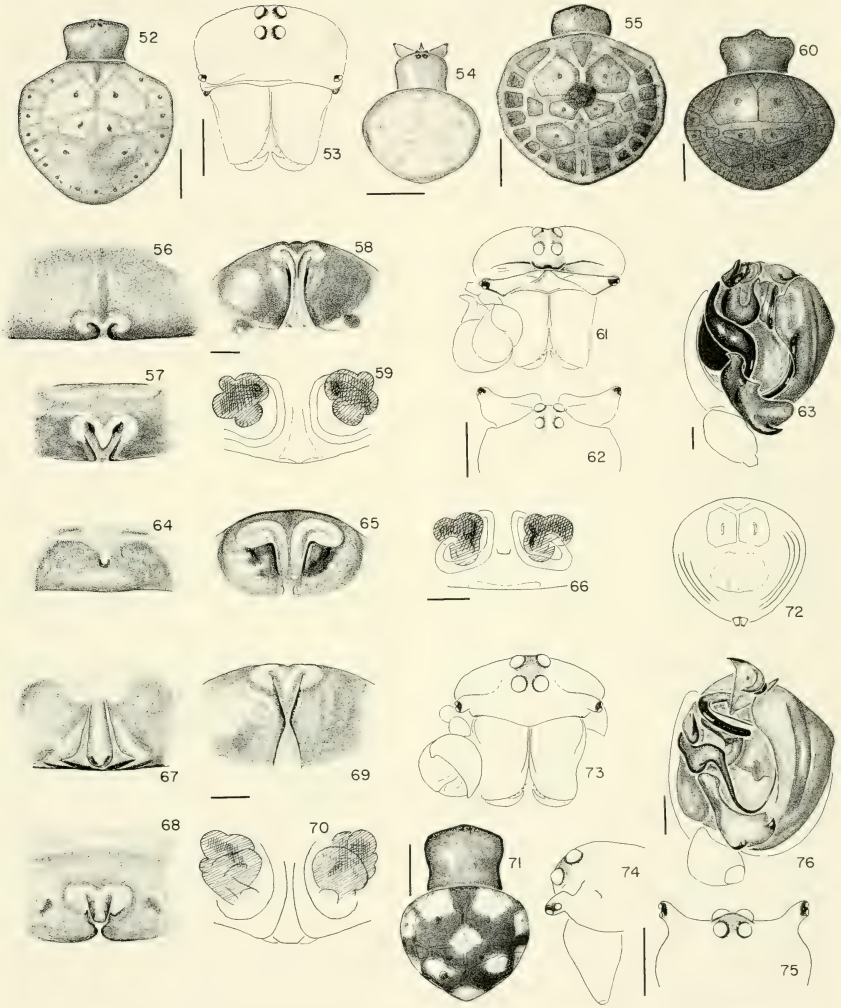
Figures 52, 53. *Hypognatha mozamba* n. sp., female. 52, dorsal. 53, eye region and chelicerae.

Figures 54, 55. *H. nasuta* O. P.-Cambridge. 54, male, dorsal. 55, female, dorsal.

Figures 56–63. *H. scutata* (Perty). 56–60, female. 56–59, epigynum. 56, ventral. 57, ventroposterior. 58, posterior. 59, cleared. 60, dorsal. 61–63, male. 61, eye region, chelicerae and right palpus. 62, eye region, subdorsal. 63, left palpus.



Figures 64–66. *H. saut* n. sp., female epigynum. 64, ventral. 65, posterior. 66, cleared.

Figures 67–76. *H. navio* n. sp. 67–72, female. 67–70, epigynum. 67, ventral. 68, ventroposterior. 69, posterior. 70, cleared. 71, dorsal. 72, abdomen, ventral. 73–76, male. 73, eye region, chelicerae and right palpus. 74, eye region and chelicera, lateral. 75, eye region, subdorsal. 76, palpus.

Scale lines. 1.0 mm; eye regions 0.5 mm; genitalia 0.1 mm.

1♂, 4 imm. (D. Silva D., MUSM); 20 Sept. 1991, 6♀, 1 imm. (D. Silva D., MUSM); 15 km E Puerto Maldonado, 12°33′S, 69°03′W, 14 July 1989, 1♀ (D. Silva D., MUSM); Zona Reservada Pakitza, 11°56′S, 71°17′W, 19 Oct. 1991, 3♀ (D. Silva D., MUSM). BRAZIL *Roraima:* Ilha de Maracá, 19–21 Mar. 1987, 3♀, 7 imm., 24 July 1987, 2♀, 2 imm. (A. A. Lise, INPA), 31 Jan.–14 Feb. 1992, 1♀, 1♂, 56 imm. (A. A. Lise, MCP 1883). *Pará:* Le Para [Belém], 8♀, 2 imm. (MNHN 2477); Belém, 1♀ (C. F. Baker, MCZ), Aug. 1971, 1♀ (M. E. Galiano, MACN); Belém, Fazenda Velha, July 1970, 4♀, 1 imm. (M. E. Galiano, MACN); Canindé, Rio Gurupi, 7–15 Apr. 1963, 14♀, 1 imm. (B. Malkin, AMNH), 7–26 Apr. 1963, 4♀, 1♂ (B. Malkin, MZSP 3304, 3360, 3388); 18 km W Canindé, Aldeia Coraci, 16–26 Apr. 1963, 3♀ (B. Malkin, AMNH); Jacareacanga, Dec. 1968, 1♀ (M. Alvarenga, AMNH); Santarém, 19♀, 26 imm. (BMNH). *Amazonas:* Boca do Sumaúma nr. Tefé, 17 Oct. 1992, 1♂ (S. H. Borges, MCN 23011a); Colosso Reserve, 80 km N Manaus, 24 Apr. 1989, 1♀ (H. Fowler, R. S. Vieira, E. Venticinque, MCZ); Reserva Flor. A. Ducke, Manaus, 26 Aug. 1992, 1♂ (J. Adis et al., INPA). *Rondônia:* Fazenda Rancho Grande, NE Cacaulandia, 6–15 Dec. 1990, 1♀ (J. E. Eger, FSCA); 15–23 March 1991, 1♀ (F. W. Skillman, FSCA). *Maranhão:* 15 km S Imperatriz, 20 Feb. 1975, 1♀ (E. S. Ross, CAS). *Ceará:* Maranguape Mountains, 1♂ (Stanford Exped., MCZ). *Goiás:* Fazenda Acéiro, Jataí, Oct. 1962, 7♀, 1♂ (Depto. Zool., MZSP 7868, 7921). *Espírito Santo:* Espírito Santo, 1♀ (USNM). *Mato Grosso:* Chapada de Guimaraes, 18 Nov. 1♀, 1 imm.; 1 Dec. 1983, 1♂ (both M. Hoffmann, MCN 11971, 11979); Chavantina, Nov. 1946, 2♀; Jan. 1947, 1♀, 17 Feb. 1947 (all H. Sick, MZSP 1236, 1244, 8048). *Mato Grosso do Sul:* Fazenda Beyou Flor, Três Lagoas, 17 Oct. 1964, 2♀ (K. Lenko, MZSP 5130); Três Lagoas, Oct. 1964, 1♀ (Exped. Depto. Zool., MZSP 3977). *São Paulo:* Itaquerê, Nova Europa, 17 Dec. 1964, 1♀, 1♂ (K. Lenko, MZSP 4073). *Paraná:* Guaíra, July 1949, 1♀ (H. Zimmermann, MZSP 9797). BOLIVIA *Cochabamba:* Yungas Chaparé, 1,900–2,800 m, 10–12 Dec. 1984, 1♀ (L. E. Peña, AMNH). *La Paz:* Cerro Uchumachi, 7 km S Coroico, 1,900 m, 16°15′S, 67°21′W, 24, 25 Nov. 1989, 2♀, 4♂ (J. Coddington et al., USNM); Yolosa, 6 Jan. 1991, P. Goloboff et al., AMNH). ARGENTINA *Misiones:* Arroyo El Central, Depto. San Antonio, Nov. 1970, 1♀ (M. E. Galiano, MACN); Cataratas de Iguazu, Aug. 1963, 1♂ (M. E. Galiano, MACN); Parque Nacional Iguazu, Jan. 1966, 1♂ (M. E. Galiano, MACN); Eldorado, Nov. 1970, 1♀ (M. E. Galiano, MACN); General Belgrano, Dec. 1972, 2♀ (M. E. Galiano, MACN).

Hypognatha saut new species
Figures 64–66; Map 2E

Holotype. Female holotype from Petit Saut, 05°07′N, 53°05′W, French Guyana, by beating vegetation above an umbrella, Oct. 1989 (E. Nance), in MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Cephalothorax orange. Abdomen dusky orange, the border darkest gray. Total length 2.8 mm. Carapace 1.42 mm long, 1.22 wide in thoracic region, 1.23 wide in cephalic region. First femur 0.80 mm, patella and tibia 1.00, metatarsus 0.66, tarsus 0.36. Second patella and tibia 0.91 mm, third 0.65, fourth 0.97. Fourth femur 1.12 mm. Abdomen 2.7 mm long, 2.9 wide.

Diagnosis. Hypognatha saut differs from *H. scutata* by having a small, ventral notch with a sclerotized rim in the center of the epigynum (Fig. 64), absent in *H. scutata* (Fig. 56), and by having the light areas on the posterior of the epigynum (Fig. 65) larger than in *H. scutata* (Fig. 58).

Specimens Examined. No other specimens were found.

Hypognatha navio new species
Figures 67–76; Map 2E

Holotype. Male holotype and female paratype from Serra do Navio, Territ. Amapá, Brazil, 0°59′S, 52°03′W, June 1966 (M. E. Galiano), in MACN. The specific name is a noun in apposition after the locality.

Description. Female paratype. Carapace orange, cephalic region darkest. Chelicerae, endites, orange. Sternum dusky orange. Legs light orange. Dorsum of abdomen with a dozen white patches, less than their diameter apart (Fig. 71), venter gray. Eyes small. Total length 3.1 mm. Carapace 1.58 mm long, 1.40 wide in thoracic region, 1.53 wide in cephalic region. First femur 0.91 mm, patella and tibia 1.09, metatarsus 0.79, tarsus 0.48. Second patella and tibia 1.04 mm, third 0.71, fourth 1.09. Fourth femur 1.05 mm. Abdomen 2.5 mm long, 2.7 wide.

Male holotype. Carapace orange, thoracic area darkest. Abdomen light orange with white pigment around the periphery, venter light orange gray. Second femur without macroseta. Total length 2.7 mm. Carapace 1.30 mm long, 1.10 wide in tho-

racic region, 1.07 wide in cephalic region. First femur 0.75 mm, patella and tibia 0.99, metatarsus 0.65, tarsus 0.40. Second patella and tibia 0.91 mm, third 0.61, fourth 0.87. Fourth femur 0.78 mm. Abdomen 2.1 mm long, 2.4 wide.

Note. Male holotype and female paratype were collected together but may not belong together. A female of *H. mozamba* was also collected with the pair.

Diagnosis. The female epigynum (Figs. 67, 68) differs from that of *H. scutata* (Figs. 56, 57) by having a median, raised, scape-like structure. The male differs by the different shape of the eye region (Figs. 73–75), the shape of the median apophysis (at 6 hr in Fig. 76), and the coiled terminal apophysis (at 11 hr in Fig. 76).

Natural History. The specimen from Venezuela was collected by sweeping in humid forest.

Specimens Examined. VENEZUELA *Bolívar*: 40 km west of Santa Elena, 1,000 m el., 7 July 1987, 1♂ (S., J. Peck, AMNH).

Hypognatha testudinaria (Taczanowski)
Figures 77–87; Map 21

Hypophthalma geometrica Taczanowski, 1879: 126, pl. 2, fig. 38, ♀. Female lectotype, two female and four immature paralectotypes, here designated, from Pumamarca [Depto. Junín], Peru, in PAN, examined. NEW SYNONYMY.

Hypophthalma testudinaria Taczanowski, 1879: 128, pl. 2, fig. 39, ♀. Male lectotype here designated, and one immature female paralectotype from Paltaypampa, one female paralectotype from Pumamarca [Depto. Junín], Peru, in PAN, examined.

Hypognatha geometrica:—Roewer, 1942: 893. Bonnet, 1957: 2258.

Hypognatha testudinaria:—Roewer, 1942: 894. Bonnet, 1957: 2259.

Note. Taczanowski described this species with two names. He had adult females and an immature male of *H. geometrica.* But he considered the immature male to be mature, describing the simple palp without sclerites as *H. geometrica,* and separated the second, *H. testudinaria,* because of the male's cephalic projections and elaborate palpi. Because males are much easier to determine than females, I use the second name *testudinaria* for this species. [There is no page priority for names that were published together (ICZN, 1985, Art. 24a, 24A).]

Description. Female lectotype of *H. geometrica.* Carapace orange-brown, sides of thoracic region darkest, chelicerae, endites brown. Sternum dark brown. Legs brown. Abdomen white with a dark brown patch on each sclerite (Fig. 82), sides white, venter dark gray. Total length 3.8 mm. Carapace 1.65 mm long, 1.39 wide in thoracic region, 1.35 wide in cephalic region. First femur 1.07 mm, patella and tibia 1.28, metatarsus 1.01, tarsus 0.52. Second patella and tibia 1.18 mm, third 0.87, fourth 1.17. Fourth femur 1.26 mm (from similar-sized female from Utcuyacu). Abdomen 3.3 mm long, 3.4 wide.

Male lectotype of *H. testudinaria.* Cephalothorax orange, except labium and sternum dusky orange, legs light orange. Abdomen gray dorsally, darker gray ventrally. Venter of second femur with a pair of minute, short macrosetae. Second tibia thicker than first and its venter with six short macrosetae, all positioned at right angle to axis of femur. Total length 2.8 mm. Carapace 1.47 mm long, 1.25 wide in thoracic region, 1.08 wide in cephalic region. First femur 1.10 mm, patella and tibia 1.36, metatarsus 1.07, tarsus 0.47. Second patella and tibia 1.22 mm, third 0.82, fourth 0.97. Fourth femur 1.04 mm. Abdomen 2.5 mm long, 2.1 wide.

Note. Males and females were collected in the same locality.

Variation. Total length of females 3.4 to 4.1 mm. The color of the dorsum of the abdomen on one paralectotype is glossy, dark brown. The median soft area of the epigynum is variable in width (Figs. 77–80). The illustrations in Figures 77, 78, and 82 were made from the female lectotype, in Figures 79, 80, and 83 from a paralectotype of *H. geometrica,* and in Figures 84–87 from the lectotype of *H. testudinaria.*

Diagnosis. The epigynum of the female is indistinct, having a median, lightly scler-

otized band (Figs. 77–80), difficult to separate from that of other lightly sclerotized females of other species. The male has a median apophysis (Fig. 87) similar to that of *H. carpish* (Fig. 94) but has a large pointed, terminal apophysis (at 9 to 2.30 hr in Fig. 87), whereas that of the similar *H. carpish* has a truncate terminal apophysis (at 9 to 12 hr in Fig. 94).

Specimens Examined. PERU *Junín:* Utcuyacu, 1,600–2,200 m, Mar. 1948, 3♀, 1 imm. (F. Woytkowski, AMNH).

Hypognatha ituara new species
Figures 88–91; Map 2N

Holotype. Female holotype from Utiariti, Mato Grosso, Brazil, 8 Aug. 1961 (K. Lenko), in MZSP no. 3732. The specific name is an arbitrary combination of letters.

Description. Female paratype. Carapace orange, chelicerae, endites, labium, sternum orange. Legs orange. Abdomen orange-white with posterior having an indistinct darker patch (Fig. 91); venter orange-gray. Total length 3.4 mm. Carapace 1.51 mm long, 1.22 wide in thoracic region, 1.19 wide in cephalic region. First femur 1.08 mm, patella and tibia 1.12, metatarsus 0.78, tarsus 0.41. Second patella and tibia 1.00 mm, third 0.66, fourth 0.91. Fourth femur 0.96 mm. Abdomen 2.8 mm long, 2.9 wide.

Diagnosis. Unlike other species, *H. ituara* has the epigynum in ventral view (Fig. 88) with a posterior sclerotized margin, and in posterior view the sclerotized lateral plates leave between them a ventral, subtriangular depression (Fig. 89).

Specimens Examined. No other specimens were found.

Hypognatha carpish new species
Figures 92–94; Map 2I

Holotype. Male holotype from west crest of Carpish Mountains, 40 mi [64 km] SW of Tingo María, Depto. Huánuco, Peru, 17 Oct. 1954 (E. I. Schlinger, E. S. Ross), in CAS. The specific name is a noun in apposition after the locality.

Note. Carpish Mountains could not be found on a map, but Carpish Pass was located at 9°42′S, 76°09′W. The area above the pass is probably above 3,000 m in elevation.

Description. Male holotype. Carapace dark orange. Chelicerae, labium, endites orange. Sternum dusky orange. Legs light orange. Dorsum of abdomen light with indistinct darker patches; venter gray. Second tibia thicker than first and its venter has six short macrosetae. Total length 2.5 mm. Carapace 1.45 mm long, 1.26 wide in thoracic region, 1.09 wide in cephalic region. First femur 1.04 mm, patella and tibia 1.30, metatarsus 1.04, tarsus 0.49. Second patella and tibia 1.20 mm, third 0.73, fourth 1.00. Fourth femur 1.04 mm. Abdomen 2.5 long, 2.4 wide.

Diagnosis. This species is similar to *H. testudinaria* but differs by having the terminal apophysis truncate (at 9 to 12 hr in Fig. 94) and having a slight median protuberance on the clypeus (Figs. 92, 93).

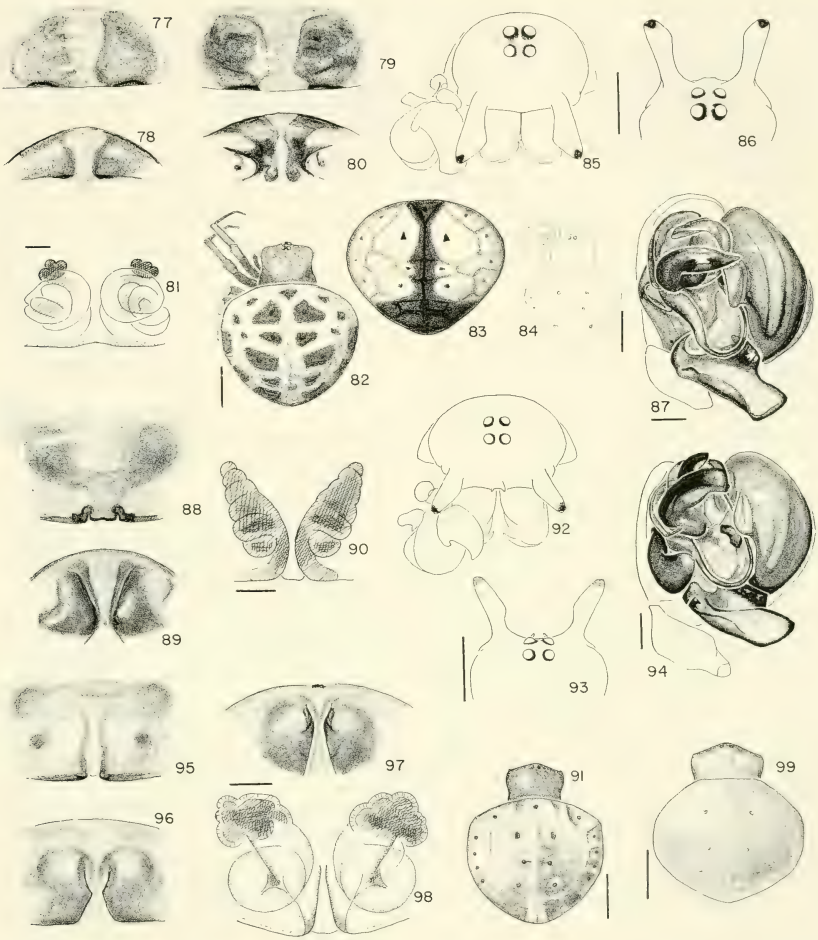
Specimens Examined. No other individuals were found.

Hypognatha mirandaribeiroi (Soares and Camargo)
Figures 95–99; Map 2N

Hypognatha mirandaribeiroi Soares and Camargo, 1948: 371, figs. 25, 26, ♀. Female holotype from Chavantina, Est. Mato Grosso, Brazil, on the riverbank of Rio das Mortes, in MZSP no. 1237, examined. Brignoli, 1983: 271.

Description. Female holotype. Cephalothorax light orange, cephalic region, and chelicerae darkest. Sternum, legs lightest. Abdomen very light orange without marks, sclerites indistinct (Fig. 99) [the individual may have just molted]. Total length 3.3 mm. Carapace 1.61 mm long, 1.49 wide in thoracic region, 1.61 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.30, metatarsus 0.91, tarsus 0.50. Second patella and tibia 1.22 mm, third 0.79, fourth 1.26. Fourth femur 1.17 mm. Abdomen 2.7 mm long, 3.1 wide.

Diagnosis. The epigynum (Fig. 95), as in *H. testudinaria,* has a median light sclerotized band, which, unlike *H. testudinaria,* has a pair of lateral plates in pos-



Figures 77–87. *Hypognatha testudinaria* (Taczanowski). 77–83, female. 77–81, epigynum. 77, 79, ventral. 78, 80, posterior. 81, cleared. 82, dorsal. 83, abdomen, dorsal. 77, 78, 82, (lectotype). 79, 80, 83, (paralectotype). 84–87, male. 84, dorsal. 85, eye region, chelicerae and right palpus. 86, eye region, subdorsal. 87, left palpus.

Figures 88–91. *H. ituara* n. sp., female. 88–90, epigynum. 88, ventral. 89, posterior. 90, cleared. 91, dorsal.

Figures 92–94. *H. carpish* n. sp., male. 92, eye region, chelicerae and right palpus. 93, eye region, subdorsal. 94, palpus.

Figures 95–99. *H.mirandaribeiroi* (Soares and Camargo), female. 95–98, epigynum. 95, ventral. 96, ventroposterior. 97, posterior. 98, cleared. 99, dorsal.

Scale lines. 1.0 mm; eye regions 0.5 mm; genitalia 0.1 mm.

terior view, leaving an hourglass-shaped depression between them (Fig. 97).

Specimens Examined. No other specimens were found.

Hypognatha tingo new species
Figures 100–102; Map 2H

Holotype. Male holotype from 69 km east of Tingo María, Depto. Huánuco, Peru, 5 Oct. 1954 (E. I. Schlinger, E. S. Ross), in CAS. The specific name is a noun in apposition after the locality.

Description. Male holotype. Carapace, chelicerae, labium, endites orange. Sternum dusky orange. Legs light orange, femora dusky. Dorsum of abdomen dusky orange; venter gray. Second femur with three short, ventral macrosetae, two in proximal half, one in distal half. Second tibia thicker than first, with three ventral macrosetae on right, four on left, two in proximal half, others in distal half. Total length 2.9 mm. Carapace 1.39 mm long, 1.17 wide in thoracic region, 1.03 wide in cephalic region. First femur 0.91 mm, patella and tibia 1.14, metatarsus 0.97, tarsus 0.44. Second patella and tibia 1.09 mm, third 0.71, fourth 0.91. Fourth femur 0.94 mm. Abdomen 2.1 mm long, 2.1 mm wide.

Diagnosis. Hypognatha tingo differs from other males by having a "vertical" groove (at 4 hr in Fig. 102) in the median apophysis, and the terminal apophysis a thin, flat, truncate sclerite (at 12 hr in Fig. 102).

Specimens Examined. No other specimens were found.

Hypognatha maria new species
Figures 103–105; Map 2H

Holotype. Male holotype from 69 km east of Tingo María, Depto. Huánuco, Peru, 12 Dec. 1954 (E. I. Schlinger, E. S. Ross), in poor physical condition, in CAS. The specific name is a noun in apposition after the locality.

Description. Male holotype. Cephalothorax orange, sternum with a dusky spot. Dorsum of abdomen dusky orange; venter gray. Second femur with three large, ventral, black macrosetae about equally spaced and at right angles to axis of article; tibia with five small, ventral macrosetae; second tibia thicker than first. Total length 2.7 mm. Carapace 1.41 mm long, 1.22 wide in thoracic region, 1.01 wide in cephalic region. First femur 0.91 mm, patella and tibia 1.18, metatarsus 1.01, tarsus 0.44. Second patella and tibia 1.07 mm, third 0.70, fourth 0.91. Fourth femur 0.96 mm. Abdomen 2.2 long, 2.0 wide.

Diagnosis. Hypognatha maria is distinguished from other species by its median apophysis with three distal prongs (at 4 hr in Fig. 105) and the terminal apophysis with a bent, "vertical", sclerite (at 11 hr in Fig. 105).

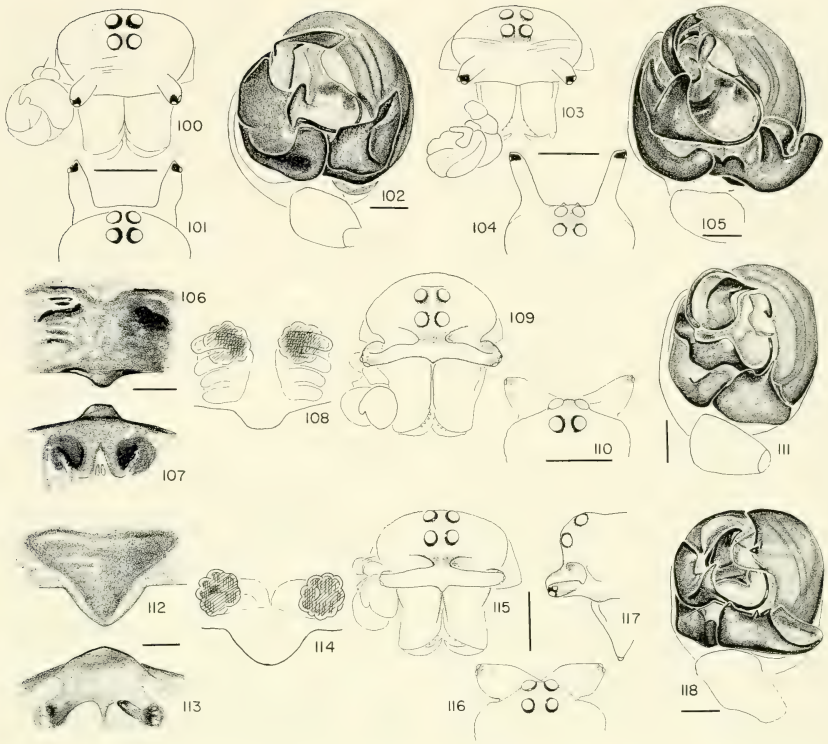
Specimens Examined. No other specimens were found.

Hypognatha viamao new species
Figures 106–111; Map 2K

Holotype. Male holotype, one female and one immature paratypes from Capivari, Viamão, Rio Grande do Sul, Brazil, 4 Feb. 1977 (E. H. Buckup), in MCN no. 5688. The specific name is a noun in apposition after the locality.

Description. Female paratype. Cephalothorax orange-brown, sternum dusky, legs lightest. Abdomen reddish brown, white and gray, venter gray, sides of venter whitish. Chelicerae with five anterior teeth, four posterior. Total length 4.3 mm. Carapace 1.44 mm long, 1.19 wide in thoracic region, 1.17 wide in cephalic region. First femur 0.93 mm, patella and tibia 1.14, metatarsus 0.75, tarsus 0.39. Second patella and tibia 1.05 mm, third 0.70, fourth 1.00. Fourth femur 1.04 mm. Abdomen 2.9 mm long, 3.2 wide.

Male holotype. Coloration lighter than in female. No macrosetae on venter of second femur. First metatarsus, second tibia and metatarsus each with a lateral keel along its posterior side. Abdomen as in female. Total length 2.9 mm. Carapace 1.30 mm long, 1.05 wide in thoracic region, 0.93 wide in cephalic region. First femur 0.81 mm, patella and tibia 1.04, metatarsus 0.75, tarsus 0.38. Second patella and tibia 0.88 mm, third 0.58, fourth 0.78. Fourth



Figures 100–102. *Hypognatha tingo* n. sp., male. 100, eye region, chelicerae and right palpus. 101, eye region, subdorsal. 102, left palpus.

Figures 103–105. *H. maria* n. sp., male. 103, eye region, chelicerae and right palpus. 104, eye region, subdorsal. 105, palpus.

Figures 106–111. *H. viamao* n. sp. 106–108, epigynum. 106, ventral. 107, posterior. 108, cleared. 109–111, male. 109, eye region, chelicerae and right palpus. 110, eye region, subdorsal. 111, palpus.

Figures 112–118. *H. cambara* n. sp. 112–114, epigynum. 112, ventral. 113, posterior. 114, cleared. 115–118, male. 115, eye region, chelicerae and right palpus. 116, eye region, subdorsal. 117, eye region, chelicera, lateral. 118, palpus.

Scale lines. Eye regions 0.5 mm; genitalia 0.1 mm.

femur 0.87 mm. Abdomen 2.08 mm long, 2.01 wide.

Note. Males and females were collected together.

Variation. Total length of females 3.1 to 4.0 mm, males 2.2 to 3.1. The illustrations were made from the female paratype (MCN 5688) and from the male holotype.

Diagnosis. Females are separated from other species by having a slight median posterior lobe in ventral view of the epigynum (Fig. 106) and, in posterior view, two dark circles separated by about the diameter of a circle or less (Fig. 107). The male can be distinguished from those of other species by its small spine on the me-

dian apophysis just to the side of the embolus (at 5 hr in Fig. 111) and, on the terminal apophysis, a pointed sclerite in the shape of a bird's head (at 12 hr in Fig. 111).

Paratypes. BRAZIL *Rio Grande do Sul:* Viamão, 27 Mar. 1966, 1♂, 3 imm. (A. A. Lise, MCN 122); 29 Dec. 1976, 2♀, 1♂, 3 imm. (A. A. Lise, MCN 4960); 24 Jan. 1977, 1♂ (A. A. Lise, MCN 5148).

Specimens Examined. BRAZIL *São Paulo:* Cubatão, Sept. 1941, 1♀, 1 imm. (Soares, MZSP 11545); Fazenda Poço Grande, Juquía; 21–26 July 1949, 1♀ (F. Lane, MZSP 11544); Represa Nova, São Bernardo, 12 Oct. 1941, 1♂ (F. Lane, MZSP). *Rio Grande do Sul:* Bom Jesus, 1 Apr. 1988, 1♂ (A. B. Bonaldo, MCN 17398); Alto dos Casemiros, Cachoeira do Sul, 25 Apr. 1993, 1♀ (R. G. Buss, MCP 3998); Campo Bom, 14 Apr. 1975, 1♀ (H. A. Gastral, M. H. Galileo, MCN 2865); Guaíba, 1 Jan. 1989, 1♂ (A. B. Bonaldo, MCN 18025); Montenegro, 11 Aug. 1977, 1♂ (A. A. Lise, MCN 6260); 29 Sept. 1977, 1♀, 1♂ (A. A. Lise, MCN 6661); 6 Oct. 1977, 1♀, 1♂, 1 imm. (H. Bischoff, E. H. Buckup, MCN 6768, 6813); 3 Nov. 1977, 2♂, 2 imm. (M. E. L. Souza, MCN 7163); 1 Dec. 1977, 1♀ (E. H. Buckup, MCN 7428); 15 Dec. 1977, 1♀, 1♂, 1 imm. (E. H. Buckup, MCZ ex MCN 7559); Muçum, 2 Mar. 1984, 1♂ (A. D. Brescovit, MCN 12109); Novo Hamburgo, 14 Dec. 1984, 1♀ (C. J. Becker, MCN 12715); Pelotas, 10 May 1967, 1♀ (P. de Biasi, MZSP 10820); São Jerônimo, 20, 21 May 1982, 1♀ (D. E. Hennig, MCN 10380); Sertão de Santana, 26 Jan. 1977, 1♂ (E. H. Buckup, MCN 5610); Triunfo, 19 May 1977, 1♂ (M. H. Galileo, MCN 5435); 23 July 1977, 1♂ (M. L. Tavares, MCN 5984); 27 Oct. 1977, 1♀ (E. H. Buckup, MCN 7033); 12 May 1981, 1♂ (E. H. Buckup, MCN 9649); 9 Dec. 1983, 1♀ (A. A. Lise, MCN 11278); 28 Nov. 1989, 1♂ (A. D. Brescovit, MCN 19037); 11 Sept. 1992, 1♂ (L. Moura, MCN 22345); 17 Oct. 1993, 1♀ (A. Francis Chini, MCN 23989); Aguas Belas, Viamão, 6 Jan. 1977, 2♀, 2 imm. (A. A. Lise, MCN 5896).

Hypognatha cambara new species
Figures 112–118; Map 2L

Holotype. Male holotype, female paratype from Itaimbézinho, Cambará do Sul, Rio Grande do Sul, Brazil, 18 May 1985 (A. A. Lise), MCN no. 13311. The specific name is a noun in apposition after the locality.

Description. Female paratype. Cephalothorax orange-brown, legs lightest. Abdomen dusky brown and white, dark gray on venter, lighter around edge. Total length 3.8 mm. Carapace 1.62 mm long, 1.36 wide in thoracic region, 1.30 wide in cephalic region. First femur 1.04 mm, patella and tibia 1.24, metatarsus 0.87, tarsus 0.45. Second patella and tibia 1.15 mm, third 0.78, fourth 1.10. Fourth femur 1.14 mm. Abdomen 3.1 mm long, 3.2 wide.

Male holotype. Coloration as in female, but with more gray pigment on sternum. Second tibiae and metatarsi each with a sclerotized ridge along center of posterior face. Second tibia with three denticles in a median posterior line. Abdomen as in female. Total length 2.9 mm. Carapace 1.34 mm long, 1.24 wide in thoracic region, 1.11 wide in cephalic region. First femur 1.00 mm, patella and tibia 1.17, metatarsus 0.83, tarsus 0.39. Second patella and tibia 1.05 mm, third 0.66, fourth 0.96. Fourth femur 0.92 mm. Abdomen 2.3 mm long, 2.3 wide.

Note. Males and females were collected together.

Variation. Total length of females 3.2 to 3.8 mm, males 2.9 to 3.0. The illustrations were made from the female paratype, and the male from the holotype.

Diagnosis. Females are distinguished from *H. viamao* by their wider lobe of the posterior margin of the epigynum (Fig. 112) and a shallow depression in posterior view and the sclerotized edge with two lobes and two small dark spots (Fig. 113). The male has a longer median apophysis with a depression along its length (at 5 hr in Fig. 118).

Paratypes. BRAZIL *Rio Grande do Sul:* Itaimbézinho, Cambará do Sul, 16 June 1983, 1♀ (A. A. Lise, MCN 11726); 18 May 1985, 3♀ (A. A. Lise, MCN 13309, 16886).

Specimens Examined. BRAZIL *Rio Grande do Sul:* Bom Jesus, 1 Apr. 1988, 1♂ (A. B. Bonaldo, MCN 17399); Cambará do Sul, 11–13 Apr. 1994, 1♀ (L. A. Moura, MCN 25499).

Hypognatha matisia new species
Figures 119–127; Map 2I

Holotype. Male holotype, one female and two male paratypes from Pakitza, Río Manu, 250 m, Depto. Madre de Dios, 12°07′S, 70°58′W, Peru, 22 Sept. 1988, from fogging *Matisia cordata* and *Hirtella triandria* trees (T. Erwin, B. D. Farrell), in MUSM, one male in USNM, one in MCZ. The specific name is a noun in apposition after the vegetation from which specimens were collected.

Description. Female paratype. Carapace brown, cephalic region orange. Chelicerae, endites, sternum orange-brown. Legs light orange. Abdomen, dorsally orange with anterior edge white, lines between plates black, and a brown patch on each large anterior plate (Fig. 122); venter gray. Abdomen with each anterior-lateral margin slightly concave (Fig.122). Total length 3.1 mm. Carapace 1.51 mm long, 1.30 wide in thoracic region, 1.30 wide in cephalic region. First femur 1.00 mm, patella and tibia 1.18, metatarsus 0.91, tarsus 0.44. Second patella and tibia 1.09 mm, third 0.74, fourth 1.04. Fourth femur 1.10 mm. Abdomen 2.6 mm long, 3.1 wide.

Male holotype. Coloration as in female. Second femur with two macrosetae close together. Second tibia thicker than first with minute ventral tubercles. Total length 2.5 mm. Carapace 1.38 mm long, 1.09 wide in thoracic region, 0.95 wide in cephalic region. First femur 0.81 mm, patella and tibia 1.11, metatarsus 0.86, tarsus 0.40. Second patella and tibia 1.00 mm, third 0.65, fourth 0.86. Fourth femur 0.87 mm. Abdomen 2.1 mm long, 2.1 wide.

Note. Males and females were collected together.

Variation. Total length of females 3.2 to 4.1 mm. The illustrations were made from female paratypes and male holotype.

Diagnosis. This species has a bicolored carapace. Females can be distinguished from others by the sclerotized, median portion of the posterior margin of the epigynum in ventral view (Fig. 119) and by the sclerotized, wider than long, plate adjacent to two slightly sclerotized rings in posterior view (Fig. 120). The male, unlike others, has a cone-shaped, projecting median apophysis (at 5 hr in Fig. 126, Fig. 127) and a large, transverse, sclerotized terminal apophysis (at 11 hr in Fig. 126).

Paratypes. PERU *Madre de Dios:* Zona Reservada de Manu, Puesto de Vigilancia Pakitza, 11°58′S, 71°18′W, 28 Sept. 1987, 1♀ (D. Silva D., J. Coddington, USNM), 2 Oct. 1987, 1♀ (D. Silva D., J. Coddington, USNM); 12 July 1992, 1♂ (D. Silva D., MUSM).

Specimens Examined. PERU *Madre de Dios:* Zona Reservada Tambopata, 290 m, 12°50′S, 69°17′W, 3 Mar. 1987, 1♀ (P. Lozada, P. USNM); 25 July 1987, 1♀ (D. Silva D., MUSM), 11 June–12 July 1988, 1♀ (D. Silva D., MUSM).

Hypognatha pereiroi new species
Figures 128–130; Map 2N

Holotype. Female holotype from Utiariti, Mato Grosso, Brazil, 25 Oct. 1966 (K. Lenko, F. S. Pereiro), in MZSP no. 6054a. The species is named after one of the collectors.

Description. Female holotype. Carapace orange, thoracic region lightest, chelicerae orange. Endites, labium, sternum, light orange; sternum dusky. Legs light orange. Abdomen light orange. Abdomen swollen as in *H. triunfo* (Fig. 174). Total length 3.5 mm. Carapace 1.56 mm long, 1.27 wide in thoracic region, 1.23 wide in cephalic region. First femur 1.04 mm, patella and tibia 1.17, metatarsus 0.83, tarsus 0.42. Second patella and tibia 1.13 mm, third 0.78, fourth 1.01. Fourth femur 1.05 mm. Abdomen 3.4 mm long, 4.1 wide.

Diagnosis. The female is distinguished from others by the triangular notch of the posterior margin of the epigynum in ventral view (Fig. 128) and, in posterior view, by two adjacent grooves narrowing ventrally (at 6 hr in Fig. 129).

Specimens Examined. No other specimens were collected.

Hypognatha belem new species
Figures 131–133; Map 2N

Holotype. Female holotype from Belém, Est. Pará, Brazil, in forest, July 1972 (D. G. McGrath), in MCN ex MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace orange, cephalic region lightest, thoracic region dusky. Chelicerae, endites, sternum orange. Legs light orange, fourth with dusky line on venter. Abdomen whitish with dusky areas, venter gray. Fourth femur only slightly longer than first. Total length 3.0 mm. Carapace 1.56 mm long, 1.26 wide in thoracic region, 1.22 wide in cephalic region. First femur 0.94 mm, patella and tibia 1.09, metatarsus 0.81, tarsus

0.44. Second patella and tibia 1.01 mm, third 0.74, fourth 0.99. Fourth femur 1.04 mm. Abdomen 0.5 mm long, 0.6 wide.

Diagnosis. *Hypognatha belem* differs from *H. matisia* by having the total length of the posterior margin sclerotized in ventral view of the epigynum (Fig. 131) and, in posterior view, having a curved sclerotized area, and in lacking apparent openings (Fig. 132).

Specimens Examined. BRAZIL St. Antonio [? Santo Antônio, Amazonas State?], no date, 2♀, 4 imm. (USNM).

Hypognatha janauari new species
Figures 134–137; Map 2N

Holotype. Female holotype, female paratype from Canal de Janauari, nr. Manaus, Amazonas State, Brazil, 16, 17 June 1987 (H. Höfer), in INPA. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace, chelicerae, endites, sternum, orange. Legs, including coxae, lighter orange. Abdomen dorsum whitish with indistinct dark median band, a dark line around margin and dark sclerotized spots in plates; venter gray without pigment. Total length 3.9 mm. Carapace 1.75 mm long, 1.47 wide in thoracic region, 1.44 wide in cephalic region. First femur 1.09 mm, patella and tibia 1.31, metatarsus 1.04, tarsus 0.48. Second patella and tibia 1.21 mm, third 0.85, fourth 1.23. Fourth femur 1.22 mm. Abdomen 3.3 mm long, 3.5 wide.

Variation. A paratype collected with the holotype has a narrower frame of the "spectacles" in posterior view of the epigynum.

Diagnosis. Unlike that of *H. matisia*, the ventral view of the epigynum has a transverse ridge (Fig. 134) and, in posterior view, larger, more sclerotized, "spectacles" (Fig. 136).

Specimens Examined. No other specimens were found.

Hypognatha elaborata Chickering
Figures 138–153; Map 2C

Hypognatha elaborata Chickering, 1953: 2, figs. 1–5, ♀, ♂. Male holotype from "Biological Area" on specimen label, "Barro Colorado Island" in publication, Panama Canal Zone, in MCZ, examined. Brignoli, 1983: 271.

Description. Female from Barro Colorado Island. Carapace dark brown. Chelicerae, sternum, coxae, legs orange-brown. Dorsum of abdomen (Fig. 145); venter dusky orange. Abdomen sclerotized, pointed behind, straight to slightly dented anteriorly (Fig. 145). Total length 3.6 mm. Carapace 1.66 mm long, 1.39 wide in thoracic region, 1.39 wide in cephalic region. First femur 1.07 mm, patella and tibia 1.26, metatarsus 0.97, tarsus 0.44. Second patella and tibia 1.18 mm, third 0.81, fourth 1.17. Fourth femur 1.10 mm. Abdomen 3.7 mm long, 3.4 wide.

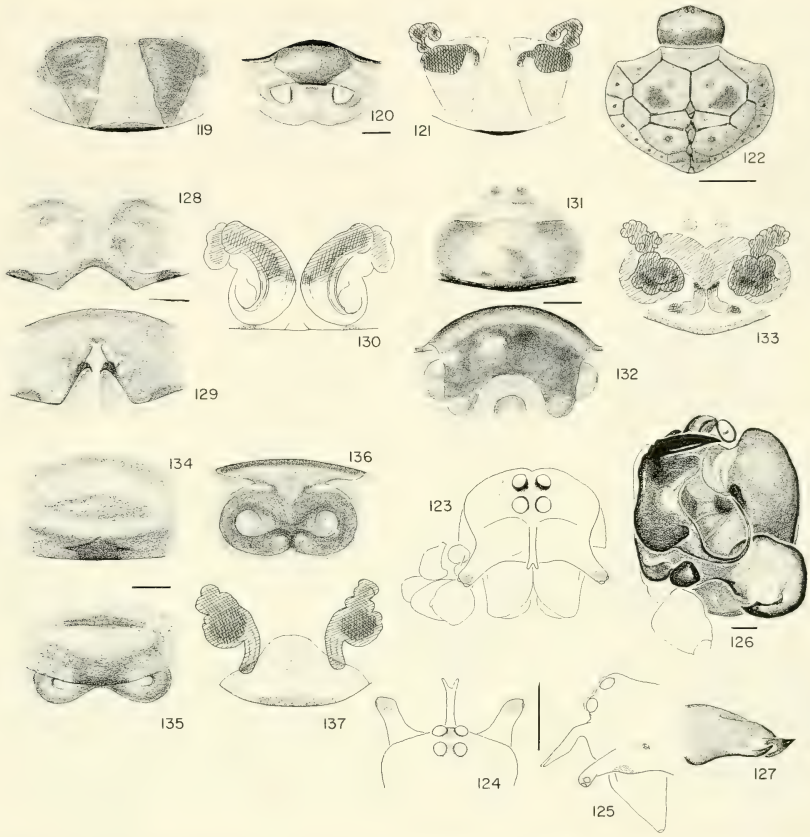
Male from Barro Colorado Island. Coloration lighter than female. Abdomen as in female (Fig. 149). Venter of second femur without macrosetae. Total length 2.7 mm. Carapace 1.43 mm long, 1.12 wide in thoracic region, 1.00 in cephalic region. First femur 1.01 mm, patella and tibia 1.30, metatarsus 1.09, tarsus 0.44. Second patella and tibia 1.15 mm, third 0.74, fourth 1.00 mm. Fourth femur 1.00 mm. Abdomen 2.3 mm long, 2.1 wide.

Note. Males and females were collected together.

Variation. Total length of females 3.1 to 3.9 mm, males 2.5 to 3.1. The duct of the vulva appears shorter in a female from Colombia than in the one illustrated (Fig. 144). The illustrations were made from several females and a male from Barro Colorado Island.

Diagnosis. The female is separated from others by the straight posterior margin of the epigynum (Fig. 142); when lifted up it shows a coil on each side of a median division (Fig. 143). The coil formed by the terminal apophysis of the male palpus is easy to see (at 11 to 1 hr in Figs. 150, 151, 153) and unlike that in any other species.

Natural History. Specimens were collected by C. E. Griswold at La Selva, Costa Rica, in successional vegetation, open vegetation, and cultivation, in understory



Figures 119–127. *Hypognatha matisia* n. sp., female. 119–121, epigynum. 119, ventral. 120, posterior. 121, cleared. 122, dorsal. 123–127, male. 123, eye region, chelicerae and right palpus. 124, eye region, subdorsal. 125, eye region, chelicera, lateral. 126, 127, left palpus. 126, ventral. 127, median apohysis, mesal.

Figures 128–130. *H. pereiroi* n. sp., epigynum. 128, ventral. 129, posterior. 130, cleared.

Figures 131–133. *H. belem* n. sp., epigynum. 131, ventral. 132, posterior. 133, cleared.

Figures 134–137. *H. janauari* n. sp., epigynum. 134, ventral. 135, ventroposterior. 136, posterior. 137, cleared.

Scale lines. 1.0 mm; eye regions 0.5 mm; genitalia 0.1 mm.

of secondary forest, and in understory of primary rain forest.

Specimens Examined. COSTA RICA Carillo [? in Guanacaste Prov. ?], 1♀ (N. Banks, MCZ). *Heredia:* El Plastico, 15 km S Puerto Viejo, 500 m, Feb. 1989, 1♀ (W. Eberhard, MCZ); La Selva nr. Puerto Viejo, 25 Mar. 1979, 1♂ (J. Coddington, MCZ); 5–20 Sept. 1981, 3♀, 1♂ (C. E. Griswold, CAS); Oct. 1981, 1♀ (C. E. Griswold, CAS); Feb. 1986, 1♀, 2♂, April 1986, 1♀, 2♂, June 1986, 1♀ (all W. Eberhard, MCZ). *Limon:* Bataan [Batán], 16 July 1956, 1♀ (N.

A. Weber, MCZ); Sixaola, 3, 4 Aug. 1981, 2♀, 3♂ (G. B. Edwards, FSCA). *Cartago:* Turrialba, 10–17 Apr., 15–30 May 1944, 2♀ (F. Schrader, AMNH). PANAMA *Chiriquí:* La Fortuna Dam Site, Sept. 1976, 1♀ (M. Robinson, MCZ). *Panamá:* nr. Gamboa, Sept. 1975, 1♀ (W. Eberhard, MCZ); Barro Colorado Island, July 1936, 1♀, Aug. 1950, 2♀, July 1954, 1♀, 2♂, 15 Aug. 1954, 1♀, May 1964, 1♀ (all A. M. Chickering, MCZ). COLOMBIA *Nariño:* La Planada, 1,800 m, 7 km S Choconés, July 1986, 2♀, 2 imm. (W. Eberhard, MCZ).

Hypognatha ica new species
Figures 154–161; Map 2H

Holotype. Male holotype, female paratype from Santo Antonio do Içá, Amazonas State, Brazil, 10 Feb. 1980 (J. M. Maia), in MCN no. 9017. The specific name is a noun in apposition after the locality.

Description. Female paratype. Carapace, chelicerae, endites, sternum orange. Legs light, dusky, orange. Abdomen gray and white, venter light orange-white, without pigment. Total length 3.7 mm. Carapace 1.69 mm long, 1.35 wide in thoracic region, 1.30 wide in cephalic region. First femur 1.04 mm, patella and tibia 1.24, metatarsus 1.01, tarsus 0.41. Second patella and tibia 1.17 mm, third 0.81, fourth 1.14. Fourth femur 1.06 mm. Abdomen 2.5 mm long, 3.1 wide.

Male holotype. Coloration as in female, but cephalic region of carapace lighter than thoracic and slightly dusky. Venter of second femur with about six small macrosetae. Total length 2.7 mm. Carapace 1.35 mm long, 1.06 wide in thoracic region, 0.93 wide in cephalic region. First femur 0.84 mm, patella and tibia 1.17, metatarsus 0.88, tarsus 0.44. Second patella and tibia 1.09 mm, third 0.71, fourth 0.89. Fourth femur 0.88 mm. Abdomen 2.0 mm long, 2.1 wide.

Note. Males and females were collected together.

Diagnosis. In *H. ica,* unlike other species, the female's epigynum, in posterior view, has a pair of light, circular depressions, separated by a swollen area wider than the diameter of a depression (Fig. 155). The median apophysis of the male palpus has a distinctive shape, with a mesally pointing tooth in ventral view of the palpus (at 5 hr in Fig. 160) and in mesal view of the median apophysis two hooks, one facing forward, the other backward (Fig. 161).

Specimens Examined. BRAZIL *Amazonas:* Benjamin Constant, 22 Sept. 1962, 1♂ (K. Lenko, MZSP 3038).

Hypognatha coyo new species
Figures 162–164; Map 2C

Holotype. Female holotype from Centr. Hidroelectrica Anchicaya, 400 m, Depto. Valle, Colombia [not dated, prob. 1970s] (W. Eberhard), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female paratype. Carapace, chelicerae, endites, labium orange. Sternum dusky orange. Legs light orange. Abdomen with area between plates indistinctly white, shading out toward sides; six central dorsal plates enclosing orange circles; venter light dusky. Total length 3.1 mm. Carapace 1.40 mm long, 1.11 wide in thoracic region, 1.05 wide in cephalic region. First femur 0.85 mm, patella and tibia 1.03, metatarsus 0.76, tarsus 0.42. Second patella and tibia 0.97 mm, third 0.67, fourth 0.91. Fourth femur 0.95 mm. Abdomen 2.3 mm long, 2.7 wide.

Diagnosis. Hypognatha coyo differs from others by the pair of looped ducts visible in posterior view of the epigynum (Fig. 163).

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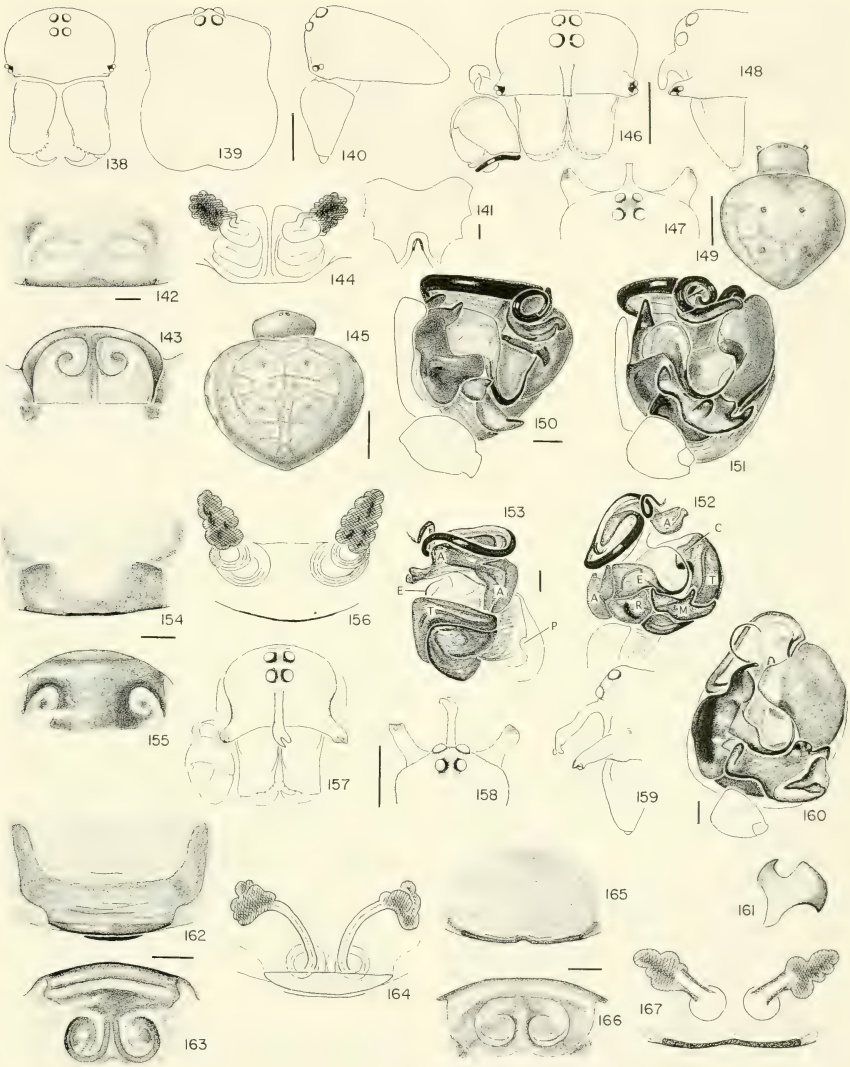
Figures 138–153. *Hypognatha elaborata* Chickering. 138–145, female. 138, eye region and chelicerae. 139, carapace. 140, carapace and chelicera, lateral. 141, sternum. 142–144, epigynum. 142, ventral. 143, posterior. 144, cleared. 145, dorsal. 146, 147, male. 146, eye region, chelicerae and right palpus. 147, eye region, subdorsal. 148, eye region, chelicera, lateral. 149 dorsal. 150–153, left palpus. 150, mesal. 151, ventral. 152, 153, pulled apart. 152, ventral. 153, dorsal.

Figures 154–161. *H. ica* n. sp. 154–156, epigynum. 154, ventral. 155, posterior. 156, cleared. 157–160, male. 157, eye region, chelicerae and right palpus. 158, eye region, subdorsal. 159, eye region, chelicera, lateral. 160, 161, palpus. 160, ventral. 161, median apophysis, mesal.

Figures 162–164. *H. coyo* n. sp., epigynum. 162, ventral. 163, posterior. 164, cleared.

Figures 165–167. *H. maranon* n. sp., epigynum. 165, ventral. 166, posterior. 167, cleared.



Abbreviations. A, terminal apophysis. C, conductor. E, embolus. M, median apophysis. P, paracymbium. R, radix. T, tegulum.
Scale lines. 1.0 mm; eye regions 0.5 mm; Figure 146 and genitalia 0.1 mm.

Specimens Examined. No other specimens were found.

Hypognatha maranon new species
Figures 165–167; Map 2I

Holotype. Female holotype from Río Alto Marañón [5°30'S, 78°33'W], betw. Río Cempa [?] and Río Nieva, [Depto. Amazonas], Peru, 10–24 Sept. 1924 (Klug) in AMNH. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace, chelicerae, endites, sternum orange; cephalic region slightly lighter. Legs light orange. Abdomen orange underlaid by white pigment spots; venter dusky. Total length 3.2 mm. Carapace 1.49 mm long, 1.24 wide in thoracic region, 1.22 wide in cephalic region. First femur 0.93 mm, patella and tibia 1.18, metatarsus 0.91, tarsus 0.41. Second patella and tibia 1.05 mm, third 0.79, fourth 1.05. Fourth femur 1.10 mm. Abdomen 2.5 mm long, 3.1 wide.

Diagnosis. In *Hypognatha maranon,* the coil visible in posterior view of the epigynum (Fig. 166) coils from the dorsal, whereas in *H. elaborata* (Fig. 143) it coils from the venter.

Specimens Examined. PERU *Loreto:* Explorama Lodge, 80 km NE Iquitos, 12–19 Mar. 1988, 1♀ (J. E. Eger, FSCA).

Hypognatha triunfo new species
Figures 168–170; Map 2M

Holotype. Female holotype from Triunfo, Rio Grande do Sul, Brazil, 12 May 1981 (Zanol), in MCN no. 9694. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace, chelicerae, endites, sternum orange. Legs light orange. Abdomen light orange with dark areas between the sclerites and a black patch posteriorly on each side, venter dusky. The abdomen appears swollen (as in *H. utari* [Fig. 174]). Total length 3.2 mm. Carapace 1.60 mm long, 1.14 wide in thoracic region, 1.26 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.18, metatarsus 1.20, tarsus 0.41. Second patella and tibia 1.05 mm, third 0.68, fourth 0.96. Fourth femur 1.04 mm. Abdomen 2.5 mm long, 2.5 wide.

Diagnosis. The epigynum of *Hypognatha triunfo* (Fig. 169), like *H. utari,* has three lighter areas in posterior view (Fig. 172) but differs from *H. utari* by having a lobe on the posterior margin in ventral view of the epigynum (Fig. 168) and two dark patches on the posterior face (Fig. 169).

Paratypes. BRAZIL *Rio Grande do Sul:* Triunfo, 25 Jan. 1990, 1♀ (M. A. L. Marques, MCN 19383).

Hypognatha utari new species
Figures 171–174; Map 2M

Holotype. Female holotype from Utiariti, Mato Grosso, Brazil, 25 Oct. 1966, one female paratype, 1–11 Nov. 1966 (K. Lenko, P. Pereiro), in MZSP, holotype no. 6054, paratype no. 3628. One paratype (6054) in MCZ ex MZSP. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace orange, cephalic region lightest. Chelicerae, endites, sternum dark orange, sternum with some dusky spots. Legs light orange. Abdomen very light orange, venter light dusky. Total length 3.8 mm. Carapace 1.47 mm long, 1.21 wide in thoracic region, 1.20 wide in cephalic region. First femur 0.96 mm, patella and tibia 1.04, metatarsus 0.81, tarsus 0.44. Second patella and tibia 0.99 mm, third 0.75, fourth 1.07. Fourth femur 1.09 mm. Abdomen 2.9 mm long, 3.7 wide.

Variation. Total length of females 3.8 to 4.0 mm. All three specimens, including

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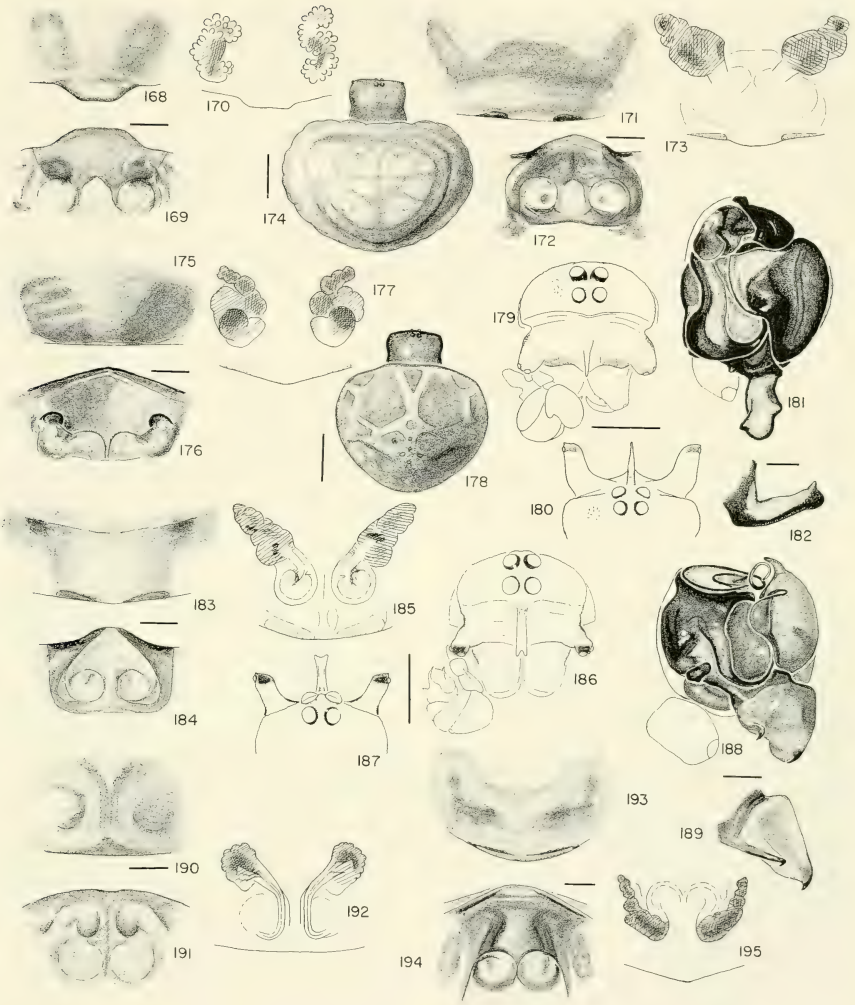
Figures 168–170. *Hypognatha triunfo* n. sp., epigynum. 168, ventral. 169, posterior. 170, cleared.

Figures 171–174. *H. utari* n. sp., female. 171–173, epigynum. 171, ventral. 172, posterior. 173, cleared. 174, dorsal.

Figures 175–178. *H. alho* n. sp., female. 175–176, epigynum. 175, ventral. 176, posterior. 177, cleared. 178, dorsal.

Figures 179–182. *H. cacau* n. sp., male. 179, eye region, chelicerae and right palpus. 180, eye region, subdorsal. 181, 182, left palpus. 181, ventral. 182, median apophysis, mesal.



Figures 183–189. *H. divuca* n. sp. 183–185, epigynum. 183, ventral. 184, posterior. 185, cleared. 186–189, male. 186, eye region, chelicerae and right palpus. 187, eye region, subdorsal. 188, 189, left palpus. 188, ventral. 189, median apophysis, mesal.

Figures 190–192. *H. rancho* n. sp., epigynum. 190, ventral. 191, posterior. 192, cleared.

Figures 193–195. *H. solimoes* n. sp., epigynum. 193, ventral. 194, posterior. 195, cleared.

Scale lines. 1.0 mm; eye region 0.5 mm; genitalia 0.1 mm.

their epigyna, are very lightly sclerotized. The illustrations were made as a composite of all three females.

Diagnosis. *Hypognatha utari* differs from *H. triunfo* by having a straight posterior margin in ventral view of the epigynum, and the ventral, sclerotized area has a pair of projections, one on each side (Fig. 171). In posterior view (Fig. 172), the epigynum lacks the two dark patches present in *H. triunfo* (Fig. 169).

Natural History. The specimen from north of Xavantina came from cerrado scrub.

Specimens Examined. BRAZIL *Mato Grosso:* 260 km N Xavantina, 12°49′S, 31°46′W, 400 m, Feb.–Apr. 1969, 1♀ (Xavantina-Cachimbo Exped., MCZ).

Hypognatha alho new species
Figures 175–178; Map 2L

Holotype. Female holotype from Fazenda Pan d' Alho, Itú, Est. São Paulo, Brazil, 17 Dec. 1960 (F. Werner, U. Martins, Harm), in MZSP no. 7396. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dusky orange, thoracic region lightest. Chelicerae, endites, labium orange. Sternum dark dusky orange. Legs light dusky orange. Abdomen (Fig. 178) orange-brown with venter brownish. Total length 3.2 mm. Carapace 1.37 mm long, 1.16 wide in thoracic region, 1.13 wide in cephalic region. First femur 0.81 mm, patella and tibia 0.97, metatarsus 0.65, tarsus 0.39. Second patella and tibia 0.85 mm, third 0.62, fourth 0.91. Fourth femur 0.86 mm. Abdomen 2.9 mm long, 2.9 wide.

Variation. Total length of females 3.0 to 4.3 mm. The illustrations were made from the female holotype.

Diagnosis. In posterior view the epigynum is distinctly concave, and on each side is a small sickle-shaped dark spot (Fig. 176).

Specimens Examined. BRAZIL *Minas Gerais:* Serra do Caraça, 23–26 Nov. 1960, 1♀ (U. Martins, MZSP 7963). *Rio de Janeiro:* Rio de Janeiro, 1♀ (ZMUC); Teresópolis, 900–1,100 m, 7–9 Nov. 1945, 2♀, 6 imm. (H. Sick, AMNH). *São Paulo:* Ilha São Sebastião, 19 Jan. 1950, 1♀, uncertain determination (H. Urban, MZSP 7697); Ilha da Cananéia, 5, 6 June 1976, 1♀ (L. R. Fontes, MZSP 13218).

Hypognatha cacau new species
Figures 179–182; Map 2G

Holotype. Male holotype from Fazenda Rancho Grande, northeast of Cacaulandia, Rondônia State, Brazil, 6–15 Dec. 1990, rainforest pantrap (G. B. Edwards), in FSCA. The specific name is a noun in apposition after the locality.

Description. Male holotype. Carapace, chelicerae, endites, labium, sternum dark orange. Legs dusky orange. Dorsum of abdomen dusky with darker dusky marks, including two curved median transverse bands; venter dusky. Body heavily sclerotized. Femora and tibiae without macrosetae. Total length 2.7 mm. Carapace 1.33 mm long, 1.07 wide in thoracic region, 0.99 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.18, metatarsus 0.86, tarsus 0.43. Second patella and tibia 1.07 mm, third 0.65, fourth 0.87. Fourth femur 0.91 mm. Abdomen 2.1 mm long, 2.1 wide.

Diagnosis. The pointed median projection of the clypeus and the shape of the median apophysis (at 6 hr in Fig. 181), with a right angle in mesal view (Fig.182), are diagnostic.

Specimens Examined. PERU *San Martín:* San Martín [nr. Juanjui (Pallister, 1956)], 15, 16 Dec. 1946, 1♂ (J. C. Pallister, AMNH).

Hypognatha divuca new species
Figures 183–189; Map 2G

Holotype. Male holotype, seven female and one male paratypes from Divisoria, 1,700 m, Depto. Huánuco [La Divisoria, Depto. Ucayali, 09°05′S, 75°46′W], Peru, 23 Sept.–3 Oct. 1946 (F. Woytkowski) in AMNH (one female in MCZ ex AMNH). The specific name is an arbitrary combination of letters.

Description. Female paratype. Carapace, chelicerae, dark orange. Endites, sternum orange. Legs orange, indistinctly ringed gray. Abdomen orange-white with sides on posterior gray, venter gray. Total length 3.1 mm. Carapace 1.63 mm long, 1.32 wide in thoracic region, 1.27 wide in cephalic region. First femur 1.01 mm, pa-

tella and tibia 1.18, metatarsus 0.88, tarsus 0.45. Second patella and tibia 1.14 mm, third 0.76, fourth 1.07. Fourth femur 1.04 mm. Abdomen 2.7 mm long, 2.9 wide.

Male holotype. Coloration as in female, but legs light orange, abdomen dusky orange. Second femur with a ventral, short macroseta at two-thirds its length. Second tibia slightly thinner than first. Total length 2.6 mm. Carapace 1.31 mm long, 1.10 wide in thoracic region, 0.96 wide in cephalic region. First femur 0.87 mm, patella and tibia 1.09, metatarsus 0.87, tarsus 0.44. Second patella and tibia 1.04 mm, third 0.68, fourth 0.91. Fourth femur 0.86 mm. Abdomen 2.1 mm long, 2.2 wide.

Note. Males and females were collected together.

Variation. The illustrations were made from female paratypes and from the male holotype.

Diagnosis. In ventral view the female has a pair of sclerotized thickenings on the posterior margin of the epigynum (Fig. 183) and, in posterior view, a triangular depression containing two posterior circles (Fig. 184). The palpus has a terminal apophysis with a coiled thread, like that of *H. elaborata*, but *H. divuca* differs by having a conical median apophysis (at 5 hr in Fig. 188, Fig. 189).

Specimens Examined. PERU *Pasco:* Huancaba, Quebrada Castillo, NW Iscozacin, 345 m, 10°10′S, 75°15′W, 6 Sept. 1987, 2♂ (D. Silva D., MUSM).

Hypognatha rancho new species
Figures 190–192; Map 2J

Holotype. Female holotype from Rancho Grande nr. Maracay [Est. Aragua], Venezuela, 15–31 Mar. 1946 (W. Beebe and others), in AMNH. The specific name is a noun in apposition after the locality.

Description. Female holotype. Cephalothorax orange. Abdomen dusky, dark orange without pattern; venter dusky. Posterior median eyes 1.4 diameters of anterior medians, laterals 0.9 diameter. Anterior median eyes 1.1 diameters apart. Posterior median eyes 1.1 diameters apart. Ocular trapezoid wider behind than in front. Height of clypeus equals 4 diameters of anterior median eye. Total length 3.0 mm. Carapace 1.56 mm long, 1.30 wide in thoracic region, 1.26 wide in cephalic region. First femur 0.93 mm, patella and tibia 1.18, metatarsus 0.81, tarsus 0.45. Second patella and tibia 1.09 mm, third 0.77, fourth 0.97. Fourth femur 1.02 mm. Abdomen 2.5 mm long, 2.5 wide.

Diagnosis. In ventral view, the epigynum has a median, Y-shaped shadow (Fig. 190); in posterior view, the epigynum is lightly sclerotized, with a pair of openings behind scale-shaped darker areas (Fig. 191).

Specimens Examined. No other specimens were found.

Hypognatha solimoes new species
Figures 193–195; Map 2D

Holotype. Female holotype from Alto Solimões, Amazonas State [nr. Benjamin Constant (Lise, personal communication)], Brazil, Dec. 1979 (A. A. Lise), in MCN no. 8896. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace orange, chelicerae dark orange. Sternum dusky orange. Legs light orange. Abdomen light orange with small white pigment spots on dorsum, venter dusky. Total length 2.8 mm. Carapace 1.53 mm long, 1.29 wide in thoracic region, 1.18 wide in cephalic region. First femur 0.96 mm, patella and tibia 1.18, metatarsus 0.87, tarsus 0.47. Second patella and tibia 1.14 mm, third 0.79, fourth 1.10. Fourth femur 1.08 mm. Abdomen 2.4 mm long, 2.7 wide.

Diagnosis. In *Hypognatha solimoes,* the posterior view of the epigynum (Fig. 194) has two circles dorsal to a sclerotized rectangle containing shadows of paired upside-down J-shaped structures.

Specimens Examined. No other specimens were found.

Hypognatha deplanata (Taczanowski)
Figures 196–207; Map 2J

Hypophthalma deplanata Taczanowski, 1873: 284, pl. 6, fig. 32, ♀. Female holotype from Cayenne, French Guyana, in PAN, examined.

Hypognatha deplanata:—Roewer, 1942: 893. Bonnet, 1957: 2258.

Description. Female holotype. Carapace, chelicerae orange. Endites, labium, sternum dusky orange-brown. Legs light dusky orange. Abdomen brown, anterior lateral corner white (Fig. 198); venter gray without marks, edge white. Total length 3.3 mm. Carapace 1.34 mm long, 1.22 wide in thoracic region, 1.14 wide in cephalic region. First femur 0.91 mm, patella and tibia 1.08, metatarsus 0.81, tarsus 0.47. Second patella and tibia 0.99 mm, third 0.76, fourth 0.97. Abdomen 2.4 mm long, 2.8 wide.

Male from Roraima. Coloration as in female, legs with broad darker rings. Posterior median eyes 1 diameter of anterior medians, laterals 0.6 diameter. Second femur with a short, ventral tooth, distally at about two-thirds of its length. Total length 3.0 mm. Carapace 1.45 mm long, 1.20 wide in thoracic region, 1.07 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.26, metatarsus 1.01, tarsus 0.47. Second patella and tibia 1.13 mm, third 0.72, fourth 1.01. Fourth femur 1.03. Abdomen 2.1 mm long, 2.6 wide.

Note. Males and females were collected together.

Variation. Total length of females 3.3 to 4.0 mm, males 2.9 to 3.1. Figures 196–198 were made from the female holotype, and Figures 199–207 from specimens from Roraima. Because only one specimen, the holotype, was available from the Guianas, there is some uncertainty as to whether or not all specimens belong to one species.

Diagnosis. The diagnostic feature of females is the median hump on the ventral face of the epigynum (Figures 196, 197, 199–201) and in posterior view a pair of dark, indistinct circles (Figures 197, 201). The male differs from others by the large trilobed median apophysis (at 4 to 5 hr in Fig. 206, Fig. 207) and the small circle, part of the terminal apophysis (at 11 hr in Fig. 206).

Specimens Examined. BRAZIL *Roraima:* Ilha de Maracá, Rio Uraricoera, 17–25 Mar. 1987, 4♀, 2♂, 16 imm. (A. A. Lise, INPA, MCN 25375, 25378); 17–25 July 1987, 6♀, 5 imm. (A. A. Lise, INPA, MCN 25377, 25380, 25381); 18–22 Aug. 1987, 3♀, 2 imm. (R. Gribel, MCN 25676, MCZ); 5–10 Dec. 1987, 2♀, 1♂, 4 imm. (E. H. Buckup, A. A. Lise, INPA, MCN 25379). *Amazonas:* Km 62 Rodovia, Manaus, Caracaraí, 18 July 1977, 1♀ (J. Grazia, MCN 9477).

Hypognatha putumayo new species
Figures 208–215; Map 2G

Holotype. Male holotype, one male and one female paratypes from Buena Vista, Depto. Putumayo, Colombia, 23–29 July 1972 (W. Eberhard) in MCZ. The specific name is a noun in apposition after the locality.

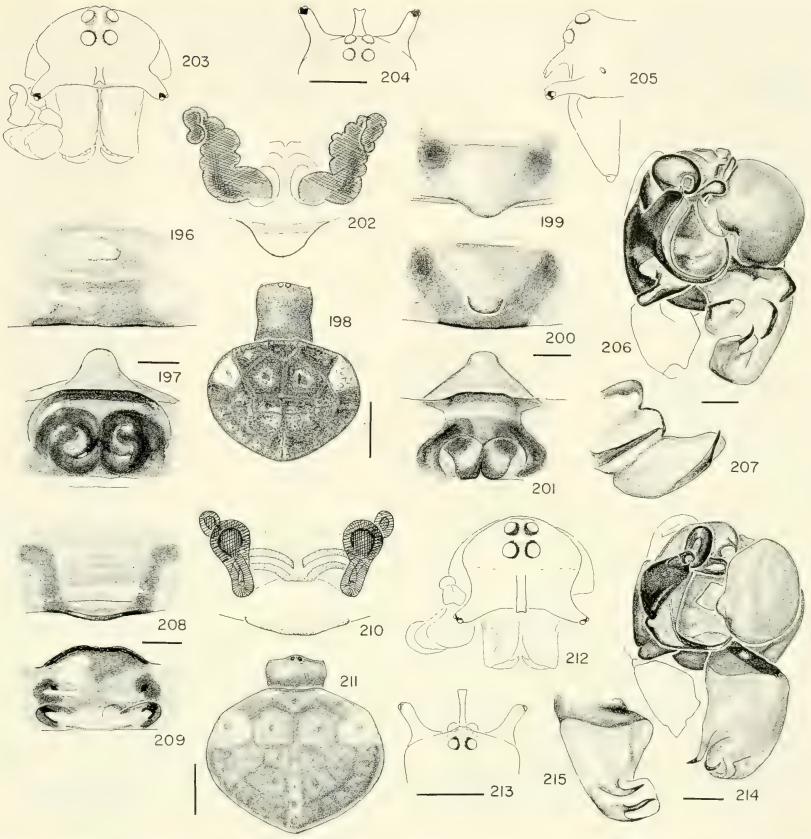
Description. Female paratype from Colombia. Carapace, chelicerae, orange-brown with a transverse darker band between cephalic and thoracic regions. Chelicerae, sternum orange-brown, sternum dusky. Legs orange. Abdomen reddish brown with some symmetrical white patches (Fig. 211), venter dark gray. Total length 3.5 mm. Carapace 1.59 mm long, 1.36 wide in thoracic region, 1.22 wide in cephalic region. First femur 1.04 mm, patella and tibia 1.18, metatarsus 0.91, tarsus 0.41. Second patella and tibia 1.11 mm, third 0.78, fourth 1.09. Fourth femur 1.09. Abdomen 2.9 mm long, 3.5 wide.

Male from Colombia. Coloration as in female. Second tibia thicker than first, proximal end of second femur with short, distal prolateral, macroseta. Total length 2.4 mm. Carapace 1.30 mm long, 1.05 wide in thoracic region, 0.91 wide in cephalic region. First femur 0.84 mm, patella and tibia 1.12, metatarsus 0.87, tarsus 0.41. Second patella and tibia 1.02 mm, third 0.65, fourth 0.90. Fourth femur 0.91 mm. Abdomen 2.1 mm long, 2.2 wide.

Note. Males and females were collected together.

Variation. Total length of females 3.1 to 3.6 mm, males 2.4 to 2.8. The illustrations were made from specimens from Colombia.

Diagnosis. The female can be separated from others by the two straight shadows of ducts, bent at their anterior ends, on the ventral surface of the epigynum (Fig. 208); in posterior view, there are no circles but two indistinct brackets. The male can be



Figures 196–207. *Hypognatha deplanata* (Taczanowski). 196–201, female. 196, 197, 199–202, epigynum. 196, 199, ventral. 198, dorsal. 200, ventroposterior. 197, 201, posterior. 202, cleared. 196–198, (holotype). 199–202, (from Roraimo State). 203–207, male. 203, eye region, chelicerae and right palpus. 204, eye region, subdorsal. 205, eye region, chelicera, lateral. 206, 207, left palpus. 206, ventral. 207, median apophysis, mesal.

Figures 208–215. *H. putumayo* n. sp. 208–211, female. 208–211, epigynum. 208, ventral. 209, posterior. 210, cleared. 211, dorsal. 212–215, male. 212, eye region, chelicerae and right palpus. 213, eye region, subdorsal. 214, 215, palpus. 214, ventral. 215, median apophysis, mesal.

Scale lines. 1.0 mm; eye regions 0.5 mm; genitalia 0.1 mm.

separated from others by the large median apophysis (at 5 hr in Fig. 214), cone-shaped with a distal flap in mesal view (Fig. 215).

Natural History. Specimens have been found on trail through forest in Sucumbíos.

Specimens Examined. ECUADOR *Sucumbíos:* Reserva Faunistica Cuyabeno, Laguna Grande, 00°00',

76°10'W, 25–29 June 1988, 2♀, 1 imm., 31 July–5 Aug. 1988, 6♀, 2 imm. (W. Maddison, MCZ).

Hypognatha colosso new species
Figures 17–19, 216–224; Map 2J

Holotype. Male holotype from Reserva Colosso, 80 km north of Manaus, Amazonas State, Brazil, 20 Sept. 1989 (H. G. Fowler, E. Venticinque, R. S. Vieira), in MCN. The specific name is a noun in apposition after the locality.

Description. Female from near Tefé. Carapace orange, cephalic region lightest. Chelicerae, endites orange, sternum dusky, orange-brown. Legs light orange, except first, second, and fourth femora gray, all tarsi gray to black. Abdomen maculated white with brown, venter light gray. Total length 3.0 mm. Carapace 1.47 mm long, 1.25 wide in thoracic region, 1.16 wide in cephalic region. First femur 0.92 mm, patella and tibia 1.09, metatarsus 0.93, tarsus 0.39. Second patella and tibia 1.05 mm, third 0.72, fourth 1.01. Fourth femur 1.05 mm. Abdomen 2.5 mm long, 2.7 wide.

Male holotype. Cephalothorax orange, legs lightest. Abdomen dorsally with white pigment spots, almost no gray, venter light gray. Second femur with distal short, ventral macroseta, tibia with six small ones. Total length 2.5 mm. Carapace 1.23 mm long, 1.10 wide in thoracic region, 0.86 wide in cephalic region. First femur 0.92 mm, patella and tibia 1.11, metatarsus 0.81, tarsus 0.42. Second patella and tibia 1.04 mm, third 0.62, fourth 0.91. Fourth femur 0.92 mm. Abdomen 2.1 mm long, 2.2 wide.

Note. Males and females were collected together.

Variation. Total length of females 3.0 to 3.8 mm. The illustrations were made from a female from Tefé and from the male holotype. Between the holotype and specimens from near Tefé are some minor differences in the shape of the palpal sclerites.

Diagnosis. The venter of the female epigynum has a diagnostic transverse ridge, best seen in ventroposterior view (Fig. 217); the male's median apophysis is distally bulkier than that of similar species.

Specimens Examined. BRAZIL *Amazonas:* Boca do Sumaúma, nr. Tefé, 17 Oct. 1992, 2♀, 1♂ (S. H. Borges, MCN 22970, 23011). *Mato Grosso:* Sinop, Feb. 1976, 2♀ (O. Roppa, AMNH).

Hypognatha furcifera (O. P.-Cambridge)
Figures 225–228

Mutina furcifera O. P.-Cambridge, 1881: 771, pl. 56, fig. 4, ♂. Male from the Amazon (Traill), in HECO, examined.

Hypognatha furcifera:—Simon, 1895a: 871, figs. 936, 937, ♂. Bonnet, 1957: 2258. Roewer, 1942: 893.

Description. Male holotype. Carapace, cephalic region, thoracic region, chelicerae, endites, sternum orange. Legs light orange. Abdomen orange-white without pigment dorsally, venter light dusky. Second femur with a short, distal, ventral, macroseta. Total length 2.7 mm. Carapace 1.30 mm long, 1.09 wide in thoracic region, 0.91 wide in cephalic region. First femur 0.90 mm, patella and tibia 1.17, metatarsus 0.76, tarsus 0.40. Second patella and tibia 1.06 mm, third 0.61, fourth 0.87. Abdomen 2.2 mm long, 2.3 wide.

Diagnosis. Hypognatha furcifera differs from other *Hypognatha* species by having a large median apophysis with four lobes (M in Fig. 227, Fig. 228) and a terminal apophysis resembling an embolus, pointing in the opposite direction and sitting within the embolus loop (Fig. 228).

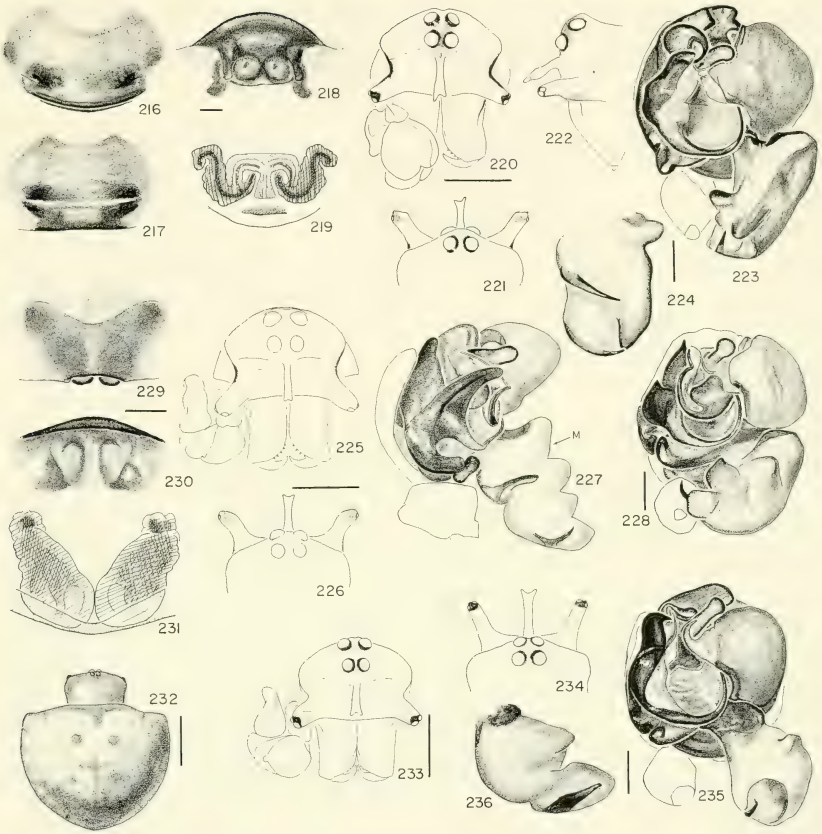
Distribution. Unfortunately it is not known where in the Amazon area the specimen was collected.

Specimens Examined. No other specimens were found.

Hypognatha tocantins new species
Figures 229–232; Map 2L

Holotype. Female holotype from Porto Nacional, Tocantins State, Brazil, 10–13 Nov. 1992 (L. Moura), in MCN no. 22628. The specific name is a noun in apposition after the locality.

Description. Female holotype. Cephalothorax orange. Chelicerae and sternum darkest. Abdomen orange with tiny white spots covering dorsum, venter dusky. Ab-



Figures 216–224. *Hypognatha colosso* n. sp. 216–219, epigynum. 216, ventral. 217, ventroposterior. 218, posterior. 219, cleared. 220–224, male. 220, eye region, chelicerae and right palpus. 221, eye region, subdorsal. 222, eye region, chelicera, lateral. 223, 224, left palpus. 223, ventral. 224, median apophysis, ventral.

Figures 225–228. *H. furcifera* (O. P.-Cambridge), male. 225, eye region, chelicerae and right palpus. 226, eye region, subdorsal. 227, 228, palpus. 227, mesal. 228, ventral.

Figures 229–232. *H. tocantins* n. sp., female. 229–231, epigynum. 229, ventral. 230, posterior. 231, cleared. 232, dorsal.

Figures 233–236. *H. jacaze* n. sp., male. 233, eye region, chelicerae and right palpus. 234, eye region, subdorsal. 235, 236, palpus. 235, ventral. 236, median apophysis, mesal.

Abbreviations. M, median apophysis.

Scale lines. 1.0 mm; eye regions 0.5 mm; genitalia 0.1 mm.

domen with anterior lateral angles (Fig. 232). Total length 3.3 mm. Carapace 1.45 mm long, 1.17 wide in thoracic region, 1.17 wide in cephalic region. First femur 1.00 mm, patella and tibia 1.17, metatarsus 0.78, tarsus 0.41. Second patella and tibia 1.04 mm, third 0.69, fourth 0.97. Fourth femur 1.01. Abdomen 2.7 mm long, 2.9 wide.

Diagnosis. In ventral view, the epigynum is covered by a sclerite with a pair of short, anteriolateral extensions (Fig. 229), and in posterior view the lightly sclerotized median area contains the shadows of two upside-down J-shaped lines (Fig. 230).

Specimens Examined. No other specimens were found.

Hypognatha jacaze new species
Figures 233–236; Map 2J

Holotype. Male holotype from Jacazeranga [? Jacaréacanga, 06°16′S, 57°39′W, Paynter, 1991], Pará State, Brazil, Oct. 1959 (M. Alvarenga), in AMNH. The specific name is an arbitrary combination of letters derived from the stated name of the locality.

Description. Male holotype. Carapace, chelicerae, sternum orange-brown. Sternum with some black pigment spots. Legs orange. Dorsum of abdomen brownish, posteriorly grading into black; venter dusky. Second femur with a ventral short macroseta. Second tibia thicker than first. Total length 2.5 mm. Carapace 1.32 mm long, 1.09 wide in thoracic region, 0.97 wide in cephalic region. First femur 0.85 mm, patella and tibia 1.17, metatarsus 0.88, tarsus 0.42. Second patella and tibia 1.05 mm, third 0.66, fourth 0.87. Fourth femur 0.91 mm. Abdomen 2.3 mm long, 2.2 mm wide.

Diagnosis. Hypognatha jacaze differs from the other *Hypognatha* species with a large soft median apophysis by having only two large lobes (at 4 hr in Fig. 235; Fig. 236) and by lacking the embolus-shaped coil of the terminal apophysis present in *H. furcifera* (Fig. 228) and *H. deplanata* (Fig. 206).

Specimens Examined. No other specimens were found.

Encyosaccus Simon

Encyosaccus Simon, 1895b: 847. Type species *E. sexmaculatus*, designated by Simon. Neave, 1939b: 229. The gender of the name is masculine (Bonnet, 1956: 1656).

Diagnosis. Female carapace as wide in eye region as in thoracic, as in *Gasteracantha.* Unlike *Gasteracantha,* carapace of male also as wide in eye region as thoracic. Sternum pointed posteriorly, between fourth coxae (Fig. 240), unlike *Gasteracantha.* Abdomen oval, wider than long, with sclerotized disks, but lacking spines. Ring around spinnerets not sclerotized. Fourth legs of female longer than first.

Genitalia. Epigynum simple, with median, pointed lobe (Fig. 241), and posterior view with sclerotized lateral plates separated by a median plate (Fig. 242).

Male palpus wider than long (as in *Xylethrus*). Palpus lacks terminal apophysis (as in *Gasteracantha* and *Xylethrus*), embolus bent, supported by conductor (at 1 hr in Fig. 247). With curved sickle-shaped paramedian apophysis (at 12 hr in Fig. 247) and small median apophysis with square projection (below the center in Fig. 247).

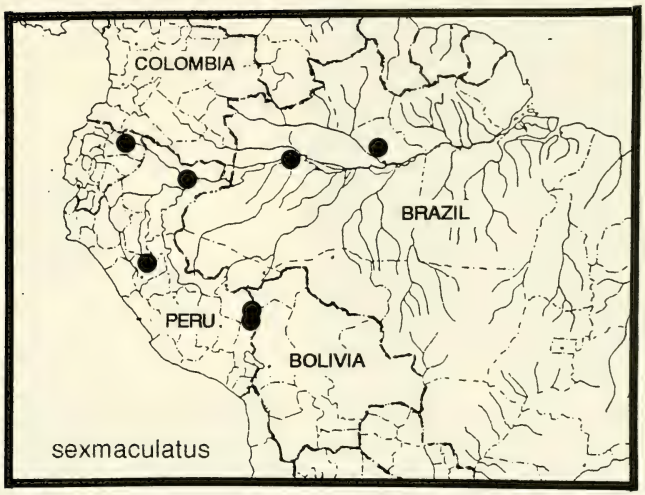
The palpus resembles that of *Spilasma,* the conductor and paramedian apophysis being similar in shape (Levi, 1995b, fig. 151). Also, the palpus is similar to that of *Micrathena nigrichelis* Strand (Levi, 1985, fig. 6).

Relationship. The elongated fourth femur is a synapomorphy of *Hypognatha, Xylethrus, Gasteracantha, Micrathena,* and *Pronous.* The square carapace and absence of terminal apophysis in the palpus are synapomorphies with *Gasteracantha.* The oval, wider than long, sclerotized abdomen is an autapomorphy of *Encyosaccus.*

Distribution. Only one species is known, from South America (Map 3).

Encyosaccus sexmaculatus Simon
Plate 1; Figures 237–247; Map 3

Encyosaccus sexmaculatus Simon, 1895b: 847, fig. 894, ♀. Female holotype from Fonte Boa, Ama-



Map 3. Distribution of *Encyosaccus sexmaculatus*.

zonas State, Brazil, in MNHN, examined. Roewer, 1942: 935. Bonnet, 1956: 1656.

Description. Female from Napo Prov., Ecuador. Carapace, chelicerae, endites, sternum bright orange-red. Legs bright orange, metatarsi and tarsi black, except proximal ends of metatarsi. Abdomen white with paired black sclerotized patches within three pairs of orange areas (Pl. 1, Fig. 244); venter bright orange; edge around abdomen with sharply defined black line. Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.6, posterior laterals 0.5 diameter. Anterior median eyes 0.7 diameter apart. Posterior median eyes their diameter apart. Ocular quadrangle slightly wider in front than behind. Height of clypeus equals 1.3 diameters of anterior median eye. Fourth legs almost equal to first leg in length. Abdomen a dorsal-ventrally flattened disk (Fig. 244), slightly wider than long, ring around spinnerets weakly sclerotized. Total length 9.4 mm. Carapace 4.4 mm long, 3.7 wide in thoracic region, 3.8 wide in cephalic region. First femur 2.7 mm, patella and tibia 3.4, metatarsus 2.1, tarsus 1.1. Second patella and tibia 3.3 mm, third 2.3. Fourth femur 2.9, patella and tibia 3.4, metatarsus 2.1, tarsus 1.1. Abdomen 7.2 mm long, 7.4 wide. Abdomen 1.03 times wider than long.

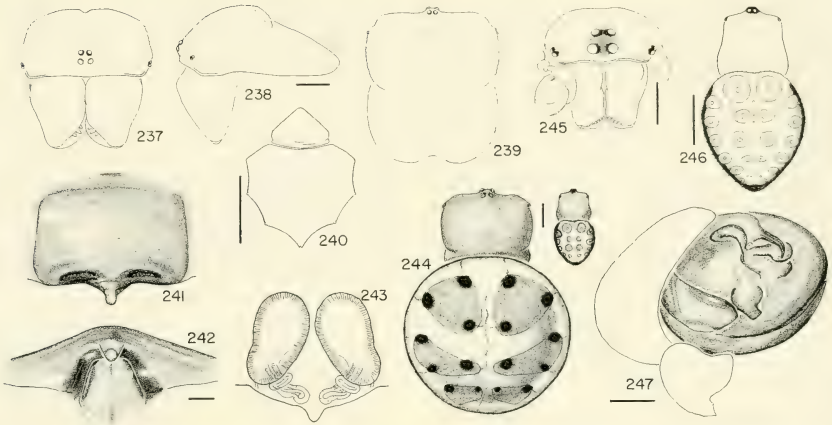
Male from Zona Reservada Tambopata, Peru. Cephalothorax orange, median eye region black, distal leg articles dusky to brown. Dorsum of abdomen orange with edge of abdomen black (Fig. 246); venter orange. Posterior median eyes 0.7 diameter of anterior medians, laterals 0.6 diameter. Anterior median eyes their diameter apart. Posterior median eyes 0.7 diameter apart. Ocular quadrangle almost square, slightly narrower behind than in front. Height of clypeus equals 0.9 diameter of anterior median eye. Endite without tooth. Palpal patella with one macroseta. First coxa without hook. Second tibia slightly S-curved. Total length 3.4 mm. Carapace 1.6 mm long, 1.4 wide, 1.2 wide behind lateral eyes. First femur 1.1 mm, patella and tibia 1.4, metatarsus 0.7, tarsus 0.5. Second patella and tibia 1.2 mm, third 0.8,

Plate 1. Upper left, web of *Hypognatha scutata* from Trinidad, 14 cm horizontal diameter of web (photo J. Coddington). Lower, female *Encyosaccus sexmaculatus* from near Iquitos, Peru (photo J. Warfel).

fourth 1.0. Abdomen 2.4 mm long, 2.2 wide.

Note. Females and males have been matched on basis of being collected together.

Variation. Total length of females 8.5 to 9.4 mm. The coloration of females is variable. The holotype has the cephalic area of the carapace black (as in Pl. 1) and the abdomen with orange patches, but without black. A specimen from near Manaus resembles the type but lacks the paired orange patches, having black disks on white. Another had black covering the median eyes and a black patch covering each of the round sclerotized disks on white. The specimen photographed (Pl. 1) has the prosoma crimson red with black, the dorsum of the abdomen with black patches on an orange field. The illustrations were



Figures 237–247. *Encyosaccus sexmaculatus* Simon. 237–244, female. 237, eye region and chelicerae. 238, carapace and chelicera, lateral. 239, carapace. 240, sternum. 241–243, epigynum. 241, ventral. 242, posterior. 243, cleared. 244, dorsal with male. 245–247, male. 245, eye region and right palpus. 246, dorsal. 247, left palpus.

Scale lines. 1.0 mm; Figure 245, 0.5 mm; genitalia 0.1 mm.

made of a female from Ecuador and a male from Depto. Madre de Dios, Peru.

Diagnosis. The shape and bright color readily separate this species from other American orb weavers. The epigynum has a simple, pointed, median lobe (Fig. 241). The palpus has the sclerotized embolus curved (Fig. 247).

Specimens Examined. ECUADOR *Napo:* Añangu, 3 June 1982, 1♀ (L. Avilés 82–2, MECN). PERU *Loreto:* 60 km N Iquitos, 1994, photo only of ♀ (Pl. 1, J. Warfel). *Huánuco:* Cucharas, Huallaga Valley, Feb.–Apr. 1954, 1♀ (F. Woytkowski, CAS). *Madre de Dios:* Alberque Cuzco Amazonico, 12°50′S, 69°05′W, 21 Feb. 1990, 1♀, 4–6 Mar. 1990, 2♀, 1♂ (D. Silva D., MUSM), 24 May 1990, 1♀ (P. Lozada, USNM); Zona Reservada Tambopata, 12°50′S, 69°17′W, 8 June 1988, 1♂ (J. Coddington, USNM). BRAZIL *Amazonas:* Km 41 Reserve, 80 km N Manaus, 1989–92, 1♀ (H. G. Fowler, MCZ); 23 May 1991, 1 imm. (H. G. Fowler, R. S. Vieira, E. Venticinque, MCZ).

Xylethrus Simon

Xylethrus Simon, 1895b: 865. Type species *X. superbus* designated by Simon. Neave, 1940: 679. The gender of the name is masculine (Bonnet, 1959: 4844).

Diagnosis. Abdomen as wide as long, or wider than long, that of male narrower. Abdomen covered with sclerotized disks, including round hemispherical tubercles (or conical ones in *X. ameda*), also with anterior, median, flat disk (Figs. 256, 268, 274). Sclerotized ring around spinnerets. Unlike other orb weavers, including *Gasteracantha, Xylethrus* has the sternum as wide as long to wider than long, truncate posteriorly between fourth coxae, and with several tubercles along edge (Figs. 251, 263, 279, 282). Male palpi wider than long (Figs. 275, 287) and, unlike that of other orb weavers, with paramedian apophysis drawn out into a thread (Figs. 276, 281, 291).

The wide palpus can be confused with that of male *Cyclosa,* but males of *Cyclosa* lack sclerotized disks on the abdomen and have the carapace with a narrow cephalic region.

Description. Female. Coloration variable, orange to brown, abdomen gray to black on underside. Lateral swellings, just behind eyes, more than two-thirds width of thoracic region of carapace (Figs. 250,

256, 261, 268). Cephalic region very high (Figs. 248, 249). Posterior median eyes usually slightly smaller than anterior medians, laterals smaller than either. Median ocular quadrangle square to wider than long. Clypeus height equals 1 to 2 diameters of anterior median eye. Fourth legs equal to, or slightly longer than, first. First and second of almost equal length.

Males. Males dwarfed, much smaller than females (Figs. 258, 270), abdomen narrower, but similar in shape (Figs. 258, 270, 274, 277, 283, 286, 290) and with similar sternum (Figs. 279, 282). Dwarf males lack endite tooth, coxal hook, modified legs. Palpal patella with one weak seta.

Genitalia. Epigynum with a simple median lobe (Figs. 252, 259, 264) and a posterior pair of depressions close to ventral margin (Figs. 253, 260, 265).

Palpus oval (Figs. 275, 280), wider than long, terminal apophysis lost (as in *Gasteracantha*), and conductor small with a transparent lobe covering sclerotized part of conductor (C in Figs. 276, 281). Embolus long (E in Figs. 276, 281) and with long paramedian apophysis pointing in opposite direction from that of embolus (PM in Figs. 276, 281). Median apophysis (M in Figs. 276, 281) small, indistinct, and lightly sclerotized.

Variation. Females, who have oviposited, with abdomen shrunken in a median longitudinal line, making abdomen U-shaped in posterior view, and with narrower transverse diameter than when fully expanded.

Relationship. The relatively wide abdomen, the sclerotized disks and sclerotized ring around the spinnerets, (Figs. 257, 262, 269) and the loss of the terminal apophysis (Fig. 276) are assumed synapomorphies with *Gasteracantha.* The fourth legs longer than first is a synapomorphy with *Micrathena.*

The hemisperical, sclerotized tubercles (Figs. 256, 261, 269), conical in *X. ameda* (Fig. 286), and the truncate posterior end of the sternum (Figs. 251, 279) are autapomorphies of *Xylethrus.* Also, the elongated, thread-shaped paramedian apophysis (PM in Fig. 276) is an autapomorphy.

Distribution. All *Xylethrus* species are Neotropical (Map 4).

Natural History. The female has been found at night in the middle of an orbweb. The hub of the web is eccentric; the web below the hub becomes narrower and longer. It appears to be very sticky. During the day females may be found on leaves, looking like bird droppings. Juveniles may hang from silk lines in dry vegetation (D. Silva D., personal communication).

Separating Species. Females are easiest to separate by the shape of the abdomen and the shape of the tubercles (Figs. 256, 261, 268). The epigynum appears variable within species (Figs. 253, 255, 265, 267). We know the males of five species but only four species of females. Only one *X. superbus* has been collected with a male, and the association of the male with the female of others is uncertain.

Key to Female *Xylethrus*

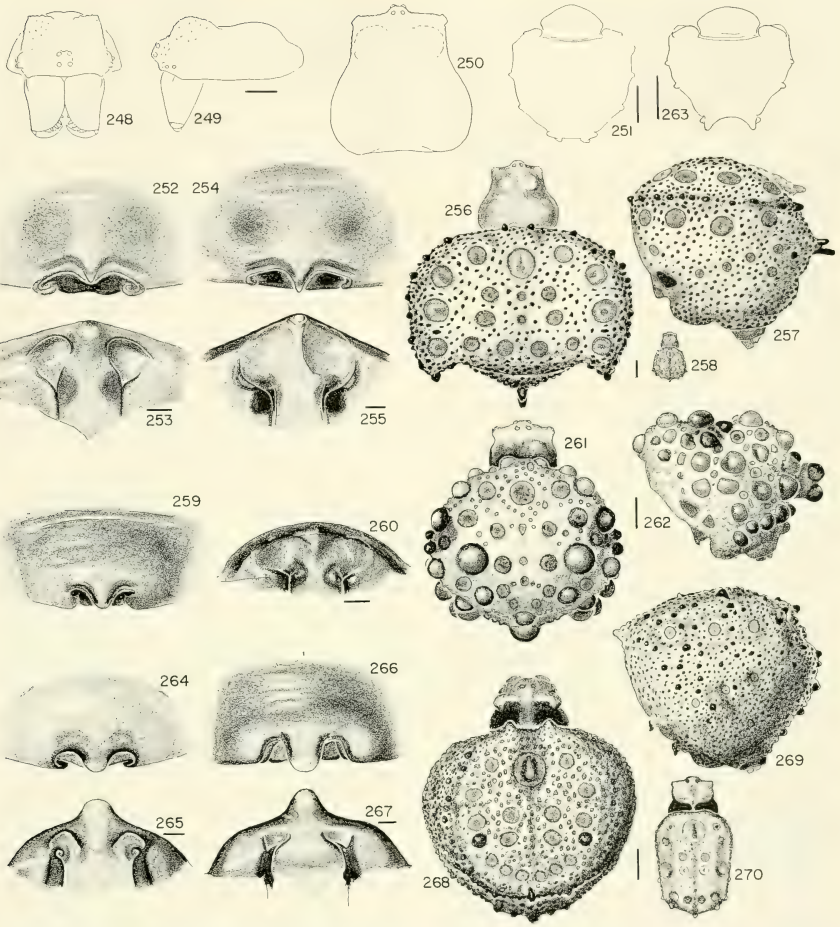
Females of *X. ameda* and *X. anomid* are not known.

1. Abdomen wider than long, with median, posterior extension and posterior lateral extensions on each side (Fig. 256, 289) 2
– Abdomen width about equal to its length, without posterior, lateral extensions (Figs. 261, 268) 3
2(1). Female from South America (Map 4A) ..... *superbus*
– Female from Mexico or Greater Antilles (Map 4D) ..... *arawak*
3(1). Large hemispherical tubercles around border of dorsum of abdomen (Fig. 261) and on sides of abdomen (Fig. 262) ..... *perlatus*
– Only tiny tubercles around border of dorsum of abdomen (Figs. 268, 269) and on sides (Fig. 269) ..... *scrupeus*

Key to Male *Xylethrus*

The association of males with females is uncertain. The male of *X. perlatus* is not known.

1. Abdomen with conical tubercles (Fig. 286) ..... *ameda*
– Abdomen with flat or hemispherical tubercles (Figs. 274, 277, 283 2
2(1). Tip of embolus of palpus curled (at 2 to 3 hr in Fig. 284) ..... *anomid*



Figures 248–258. *Xylethrus superbus* Simon. 248–257, female. 248, eye region and chelicerae. 249, carapace and chelicera, lateral. 250, carapace. 251, sternum. 252–255, epigynum. 252, 254, ventral. 253, 255, posterior. 252, 253, (lectotype). 254, 255, (from Depto. Madre de Dios, Peru). 256, dorsal. 257, abdomen lateral. 258, male, same magnification as female.

Figures 259–262. *X. perlatus* Simon, female. 259, 260, epigynum. 259, ventral. 260, posterior. 261, dorsal. 262, abdomen, lateral.

Figures 263–270. *X. scrupeus* Simon. 263–259, female. 263, sternum. 264–267, epigynum. 264, 266, ventral. 265, 267, posterior. 264, 265, (lectotype). 266, 267, (from Depto. Madre de Dios, Peru). 268, dorsal. 269, abdomen, lateral. 270, male, dorsal, same magnification as female.

Scale lines. 1.0 mm; Figures 248–251, 263, 0.5 mm; genitalia 0.1 mm.

– Embolus straight (Figs. 275, 280, 287, 291) 3

3(2). Abdomen as wide as long or wider than long (Figs. 274, 290) 4

– Abdomen longer than wide (Fig. 277); embolus an undulating thread (Fig. 280) ..... *scrupeus*

4(3). Paramedian apophysis thread-shaped (Fig. 275); South America (Map 4A) .... *superbus*

– Paramedian apophysis sickle-shaped (Fig. 291); Mexico, Greater Antilles (Map 4D) ..... *arawak*

Xylethrus superbus Simon
Figures 248–258, 271–276; Map 4A

Xylethrus superbus Simon, 1895b: 865; 1895b: 158, figs. 926 ♀, 927 ♂. Female lectotype, male and immature paralectotypes from São Paulo, Brazil [São Paulo de Olivença, Amazonas State], in MNHN no. 8195, examined. Roewer, 1942: 951. Bonnet, 1959: 4844.

Xylethrus trifidus Simon, 1895a: 157. Immature holotype from Paraguay in MNHN, examined. Roewer, 1942: 951. Bonnet, 1959: 4844. NEW SYNONYMY.

Xylethrus peruanus Archer, 1971: 157, figs. 1, 2, ♀. Female holotype from Moyabamba, Depto. San Martín, Peru, in AMNH, examined. Brignoli, 1983: 249. NEW SYNONYMY.

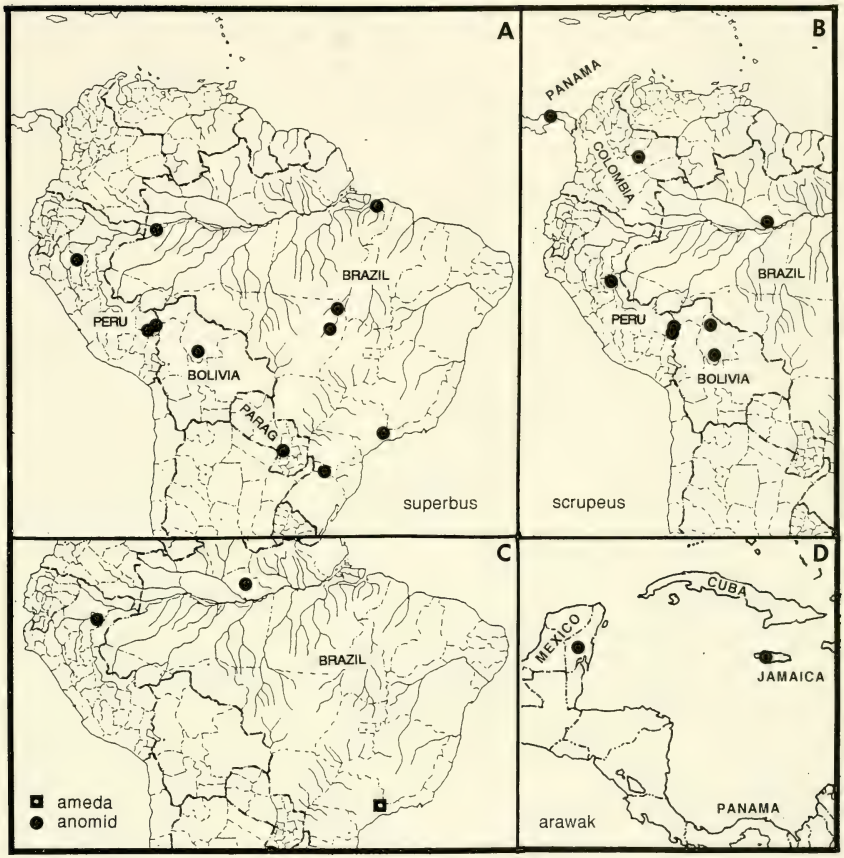
Note. The male paralectotype collected with the female *X. superbus,* and illustrated by Simon, is a male of an *Enacrosoma* species. The holotype of *X. trifidus* is an early instar, probably female, about 3 mm total length. The dorsal outline of the individual is as in an adult *X. superbus.* Archer's specimen of *X. peruanus* is a female *X. superbus.*

Description. Female from Depto. Madre de Dios, Peru. Cephalothorax reddish orange. Abdomen orange with circular sclerites, orange spinnerets and ring around spinnerets and many brown to black hemispherical spots. Carapace with two humps in cephalic region, and surface of cephalic region with grainy sculpturing (Figs. 248–250). Posterior median eyes 0.9 diameter of anterior medians, laterals 0.8 diameter. Anterior median eyes 1 diameter apart. Posterior median eyes 1.1 diameters apart. Ocular quadrangle square. Height of clypeus equals 1.5 diameters of the anterior median eye. Abdomen wider than long with posterior median and lateral extensions (Figs. 256, 257). Sclerotized ring around spinnerets (Fig. 257) broken anteriorly, and sometimes broken into several sclerites, as in a necklace. First two tibiae slightly S-shaped, metatarsi slightly curved. Total length 15.0 mm. Carapace 4.8 mm long, 4.5 wide in thoracic region, 3.0 wide in cephalic region. First femur 3.4 mm, patella and tibia 4.2, metatarsus 2.2, tarsus 1.1. Second patella and tibia 4.2 mm, third 3.7. Fourth femur 4.0 mm, patella and tibia 4.7, metatarsus 2.4, tarsus 1.1.

Male from Depto. Madre de Dios, Peru. Carapace orange-brown, eyes without black pigment. Chelicerae, labium, endites orange. Sternum light orange. Legs orange with indistinct darker rings. Abdomen orange, some white pigment between large sclerites and an indistinct longitudinal black band on each side and through middle; venter orange. Posterior median eyes same diameter as anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.7. Anterior median eyes their diameter apart. Posterior median eyes 1.1 diameters apart. Median ocular quadrangle almost square, slightly wider behind than in front. Height of clypeus equal to 1 diameter of anterior median eye. Abdomen as wide as long (Figs. 258, 274). Total length 3.0 mm. Carapace 1.38 mm long, 1.14 wide in thoracic region, 1.04 wide in cephalic region. First femur 0.81 mm, patella and tibia 1.04, metatarsus 0.46, tarsus 0.40. Second patella and tibia 1.01 mm, third 0.84. Fourth femur 1.00 mm, patella and tibia 1.04, metatarsus 0.49, tarsus 0.40.

Note. The only male was collected with a female. As in the female, the abdomen of the male is wider than that of other male *Xylethrus* species, except for *X. arawak.*

Variation. Total length of females 7.6 to 13.0 mm. The epigynum is quite variable in posterior view (Figs. 253, 255). Illustrations were made from specimens from Madre de Dios, Peru, and Figures 252 and 253 from the lectotype.



Map 4. Distribution of *Xylethrus* species.

Diagnosis. The abdomen is wider than that of other species, except *X. arawak,* and has a posterior pair of lateral extensions and a median extension (Fig. 282). The Amazonian and Brazilian distribution separates *X. superbus* from the Caribbean and Mexican *X. arawak.* The male differs from others by having the abdomen about as wide as long (Figs. 258, 274) and, unlike *X. arawak* (Fig. 291), has a thread-shaped paramedian apophysis (PM in Fig. 276) whereas that of *X. arawak* is sickle-shaped (Fig. 291). Also, the male lacks a slight constriction of the median apophysis (M in Fig. 276) present in *X. arawak.*

Natural History. The male was collected at night with the female, the male under a leaf. Another male (not in the available collections) was under another leaf nearby, 130 cm above ground (information

from specimen labels). One immature specimen was collected in cerrado scrub in Mato Grosso.

Specimens Examined. BRAZIL *Pará:* Fazenda Velha, Belém, Aug. 1970, 1 imm. (M. E. Galiano, MACN). *Goias:* Araguari [?], Mar. 1930, 2♀ (R. Spitz, MZSP 7718). *Mato Grosso:* 260 km N Xavantina, 12°49′S, 51°46′W, 400 m, Apr. 1969, 1 imm. (Xavantina-Cachimbo Exped., MCZ); Barra do Tapirape, 11–30 Nov. 1960, 1♀ (B. Malkin, AMNH). *São Paulo:* Barueri, 10 July 1966, 1 imm. (K. Lenko, MUSP 9603). *Santa Catarina:* Res. Biol. Mar. Arvoredo, 13, 14 Oct. 1994, 1 imm. (A. Braul, MCP 5093). PERU *Madre de Dios:* 15 km E Puerto Maldonado, 200 m, 12°33′S, 69°03′W, 1♀; Zona Reservada Pakitza, 356 m, 11°56′S, 71°17′W, 1–9 Oct. 1991, 1♀, 1♂, 17 Oct. 1991, 1♀ (all D. Silva D., MUSM); Zona Reservada de Manu, Río Troche, 11°58′S, 71°18′W, 5 Oct. 1987, 1 imm. (J. Coddington, USNM). BOLIVIA *El Beni:* Estación Biologico Beni, 14°47′S, 66°15′W, 8–14 Sept. 1989, 2♀ (J. Coddington et al., USNM). PARAGUAY *La Cordillera:* San Bernardino, 1♀ (E. Reimoser, MCZ).

Xylethrus perlatus Simon
Figures 259–262

Xylethrus perlatus Simon, 1895a: 158. Female holotype from Mato Grosso, Brazil, in MNHN no. 10555, examined. Roewer, 1942: 951. Bonnet, 1959: 4844.

Note. Unfortunately the type locality is not specific. Mato Grosso is a vast area of Brazil and, at the time of the descriptions, included other states to the northwest and south of the present Mato Grosso State.

Description. Female holotype. Carapace brown, eye region orange. Chelicerae orange to brown. Labium, endites orange. Sternum orange with darker edge. Coxae orange; legs orange, ringed brown. Abdomen orange to brown with a black patch on each side. Posterior median eyes subequal to anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.8. Anterior median eyes 1.5 diameters apart. Posterior median eyes 1.3 diameters apart. Ocular quadrangle rectangular, slightly wider than long. Height of clypeus equals 2 diameters of anterior median eye. Abdomen with flat disks and numerous paired, hemispherical protuberances (Figs. 261, 262). Ring around spinnerets broken anteriorly. Total length 7.3 mm. Carapace 2.7 mm long, 2.9 wide in thoracic region, 2.5 at lateral eyes. First femur 2.3 mm, patella and tibia 2.7, metatarsus 1.6, tarsus 0.8. Second patella and tibia 2.7 mm, third 2.2. Fourth femur 2.4 mm, patella and tibia 2.9, metatarsus 1.4, tarsus 0.9. Abdomen 5.6 mm long, 5.6 wide.

Variation. The animal was apparently collected after producing eggs and is caved in, making the abdomen U-shaped in dorsal view, the sides up, the center down. A similar collapse of the dorsal shape was also seen in some *X. scrupeus* and *X. superbus* specimens.

Note. Xylethrus anomid might be the male of this species.

Diagnosis. The many large hemispherical tubercles on the abdomen (Figs. 261, 262) separate this from *X. scrupeus.*

Specimens Examined. No other specimens were collected.

Xylethrus scrupeus Simon
Figures 263–270, 277–281; Map 4B

Xylethrus scrupeus Simon, 1895a: 159. Female lectotype, three immature and one male paralectotypes from Amazon State, Pará, Bahia and Mato Grosso; female lectotype here designated from the Amazon, in MNHN no. 7994, examined. Roewer, 1942: 951.

Xylethrus scrupens [sic]:—Bonnet, 1959: 4844.

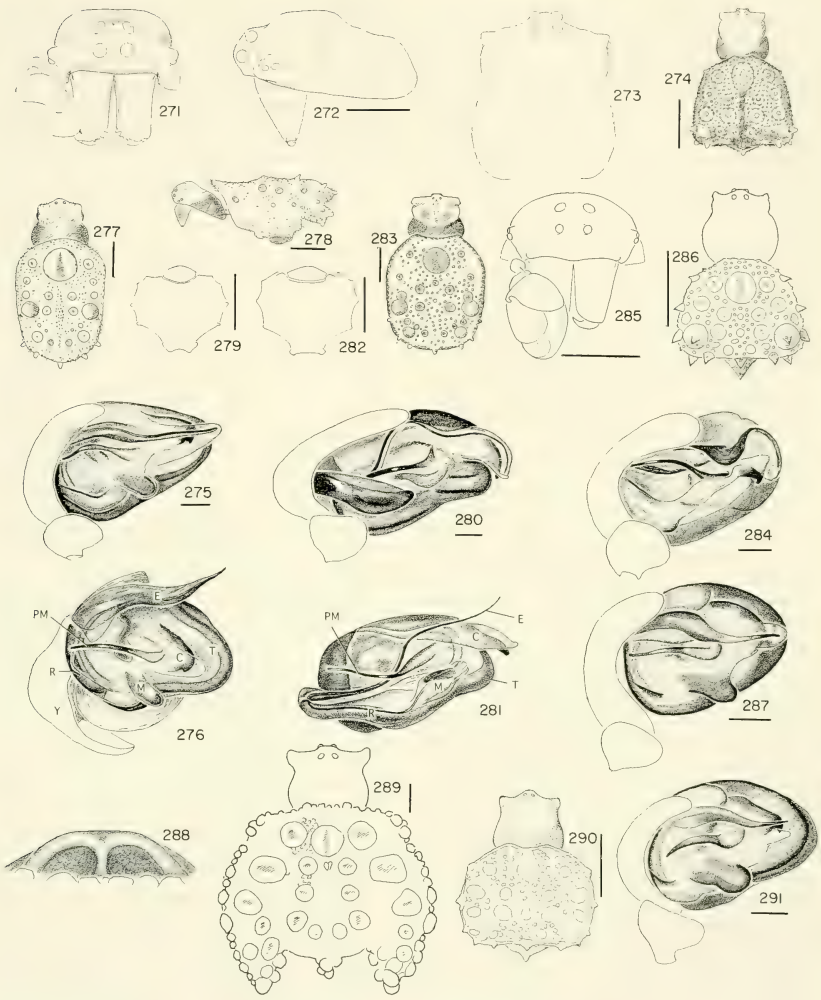
Note. The male paralectotype is described below as a new species *Xylethrus anomid.*

Description. Female from Depto. Madre de Dios, Peru. Carapace, cephalic region brown, thoracic region black, separated by an orange transverse line (Fig.

→

Figures 271–276. *Xylethrus superbus* Simon, male. 271, eye region, chelicerae and right palpus. 272, carapace and chelicera. 273, carapace. 274, dorsal. 275, left palpus. 276, palpus, pulled apart.

Figures 277–281. *X. scrupeus* Simon, male. 277, dorsal. 278, lateral. 279, sternum and labium. 280, palpus. 281, palpus bulb, pulled apart.



Figures 282–284. *X. anomid* n. sp., male. 282, sternum and labium. 283, dorsal. 284, palpus.

Figures 285–287. *X. ameda* n. sp., male. 285, eye region, chelicerae and right palpus. 286, dorsal. 287, palpus.

Figures 288–291. *X. arawak* n. sp. 288, 289, female (after Archer). 288, epigynum, posterior. 289, dorsal. 290, 291, male. 290, dorsal. 291, palpus.

Abbreviations. C, conductor. E, embolus. M, median apophysis. PM, paramedian apophysis. R, radix. T, tegulum. Y, cymbium.

Scale lines. 1.0 mm; genitalia 0.1 mm; Figures 271–273, 279, 282, 285, 0.5 mm.

268). Chelicerae, labium, endites dark brown, sternum orange with black rim and three indistinct black patches. Coxae, legs dark brown, ringed orange. Abdomen dark reddish brown. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.5 diameter. Anterior median eyes 1 diameter apart. Posterior median eyes 2.5 diameters apart. Ocular trapezoid wider than long, wider behind than in front. Height of clypeus equals 0.5 diameter of the anterior median eye. Abdomen with complete, sclerotized ring around spinnerets (Fig. 269). Total length 9.0 mm. Carapace 3.4 mm long, 3.3 wide in thoracic region, 2.7 wide in cephalic region. First femur 2.5 mm, patella and tibia 2.8, metatarsus 1.6, tarsus 0.8. Second patella and tibia 2.8 mm, third 2.7. Fourth femur 3.1 mm, patella and tibia 3.2, metatarsus 1.7, tarsus 0.9.

Male from Chacobo Indian Village, Bolivia. Carapace orange, posterior black with white setae and a pair of brown patches in cephalic region. Chelicerae, sternum orange. Legs brown with indistinct orange rings. Abdomen speckled brown and orange. Posterior median eyes same diameter as anterior medians, laterals 0.6 diameter. Anterior median eyes 1.5 diameters apart. Posterior median eyes 2 diameters apart. Ocular trapezoid wider than long and wider behind than in front. Height of clypeus equal to 1.5 diameters of anterior median eye. Total length 4.8 mm. Carapace 1.8 mm long, 1.6 wide in thoracic region, 1.2 wide in cephalic region. First femur 1.1 mm, patella and tibia 1.3, metatarsus 0.7, tarsus 0.5. Second patella and tibia 1.3 mm, third 1.2. Fourth femur 1.3 mm, patella and tibia 1.4, metatarsus 0.7, tarsus 0.5.

Note. The match of males to females is uncertain. Males and females were matched because adult males were found on Barro Colorado Island, Panama, with immatures, which were believed to be *X. scrupeus*. Also, there are no records of species other than *X. scrupeus* from northwestern South America.

Variation. Total length of females 7.7 to 9.6 mm, males 4.5 to 4.8. The illustrations were made from a female from Madre de Dios, Peru, and Figures 264 and 265 from the lectotype. The male from Bolivia was illustrated (Figs. 277–280), and the expanded palpus (Figs. 281) from a male from Panama.

Diagnosis. Unlike *X. superbus*, the female of *X. scrupeus* has a subspherical abdomen (Figs. 268, 269) and, unlike *X. perlatus* (Figs. 261, 262), lacks large hemispherical tubercles on the abdomen (Figs. 268, 269). The palpus differs by having the embolar thread undulating (Fig. 280).

Specimens Examined. PANAMA *Panamá:* Barro Colorado Island, Jan. 1936, 1♂ (J. A. Griswold, MCZ); July 1936, 2 imm., 15 Jan. 1958, 1♂ (both A. M. Chickering, MCZ). COLOMBIA *Meta:* Finca Chenevo, 20 km N Río Muco, 20 km S El Porvenir, 170 m, 1978, 1♀ (W. Eberhard, MCZ). PERU *Ucayali:* Pucallpa, 2 Oct. 1954, 1♀ (E. I. Schlinger, E. S. Ross, CAS). *Madre de Dios:* 15 km E Puerto Maldonado, 12°33′S, 69°03′W, 24 June 1989, 1♀ (D. Silva D., MUSM); Zonas Reservada Tambopata, 12°50′S, 69°17′W, 13 June 1988, 2 imm., 1♀ (MCZ ex MUSM); 20 Sept. 1991, 1♀ (D. Silva D., MUSM); 12 June 1988, 1 imm. (J. Coddington, USNM). BRAZIL *Amazonas:* Reserva Ducke, Manaus, 2 Aug. 1991, 1♀ (H. Küchmeister, LNK). BOLIVIA *El Beni:* Estación Biologico Beni, 14°47′S, 66°15′W, 8–14 Nov. 1989, 2♀ (J. Coddington et al., USNM); Chacobo Indian Village, Río Benicito, 12°30′S, 66°00′W, 31 Aug. 1960, 1♂ (B. Malkin, AMNH).

Xylethrus anomid new species
Figures 282–284; Map 4C

Holotype. Male holotype from Dimona Reserve, ca. 80 km N Manaus, Amazonas, Brazil, 1989–92 (H. G. Fowler) in MCN. The specific name is derived from the locality spelled backward.

Male holotype. Carapace orange with thoracic region dark brown, an anterior median longitudinal band and two dark patches posteriorly in cephalic region. Sternum orange with brown rim, legs ringed brown and orange. Abdomen light beige with brown spots. Posterior median eyes 1.2 diameters of anterior medians, laterals 0.8 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 1.8 diameters apart. Laterals separated by their radius. Ocular trapezoid wider than

long, wider behind than in front. Height of clypeus equal to 1.5 diameters of anterior median eye. Total length 4.8 mm. Carapace 1.9 mm long, 1.7 wide in thoracic region, 1.4 wide in cephalic region. First femur 1.2 mm, patella and tibia 1.4, metatarsus 0.8, tarsus 0.5. Second patella and tibia 1.5 mm, third 1.3. Fourth femur 1.4 mm, patella and tibia 1.5, metatarsus 0.8, tarsus 0.5.

Diagnosis. The distal curl of the embolus (at 2 to 3 hr in Fig. 284) separates *X. anomid* from all other *Xylethrus* species.

Note. The male paralectotype of *X. scrupeus*, of uncertain locality, belonged to this species. This may be the male of *X. perlatus*.

Specimens Examined. PERU *Loreto:* Alto Río Samiria, 05°07′S, 75°28′W, 15 May 1990, 1♂ (D. Silva D., MUSM).

Xylethrus ameda new species
Figures 285–287; Map 4C

Holotype. Male holotype from Diadema, São Paulo State, Brazil, 11 Feb. 1961 (P. de Biasi) in MZSP no. 8373. The specific name is an arbitrary combination of letters derived from the locality spelled backward.

Description. Male holotype. Carapace brown, thoracic region lightest. Chelicerae orange-brown. Labium, endites orange, proximally brown. Sternum orange with brown rim; brown extending at coxal insertions, brown patch behind labium. Coxae orange; legs orange and brown, indistinctly ringed. Dorsum of abdomen brown, a pair of white patches anteriorly under the integument; venter black. Posterior median eyes 1.3 diameters of anterior medians, anterior laterals 0.8 diameter, posterior laterals 1 diameter. Anterior median eyes 1.2 diameters apart. Posterior median eyes 0.8 their diameter apart. Ocular quadrangle about square, slightly wider behind than in front. Height of clypeus equals 1.8 diameters of anterior median eye. Cephalic region low. Abdomen widest posteriorly (Fig. 286). Total length 2.4 mm. Carapace 1.17 mm long, 1.06 wide, 0.80 wide behind lateral eyes. First femur 0.87 mm, patella and tibia 1.04, metatarsus 0.53, tarsus 0.42. Second patella and tibia 1.03 mm, third 0.82. Fourth femur 0.93 mm, patella and tibia 0.96, metatarsus 0.50, tarsus 0.42.

Diagnosis. This species differs from other *Xylethrus* by having conical rather than hemispherical tubercles (Fig. 286).

Specimens Examined. No other specimens were found.

Xylethrus arawak Archer
Figures 288–291; Map 4D

Xylethrus arawak Archer, 1966: 130, figs. 6, 7, ♀. Female holotype from Manchester Grove Place [Grove Place, Manchester Parish], Jamaica, West Indies, in SMIJ, lost [also not in AMNH]. Brignoli, 1983: 249.

Description. Female (from Archer). Total length 7.9 mm. Carapace 3.1 mm long, 2.3 wide, Abdomen 6.0 mm long, 6.3 mm wide.

Male. Carapace orange to brown. Clypeus, chelicerae orange. Labium, endites. Sternum orange with brown. Legs orange with brown rings. Abdomen orange and brown (Fig. 290). Posterior median eyes 1.1 diameters of anterior medians, anterior laterals 0.6 diameter, posterior laterals 0.8. Anterior median eyes their diameter apart. Posterior median eyes 1.1 diameters apart, their diameter from laterals. Ocular quadrangle slightly wider behind than in front. Height of clypeus equals 1.4 diameters of anterior median eye. Endite without tooth. Palpal patella with no macroseta. First coxa without hook. Second tibia thicker than first. Abdomen wider than long (Fig. 290). Total length 2.7 mm. Carapace 1.27 mm long, 1.12 wide, 1.01 wide in cephalic region. First femur 0.88 mm, patella and tibia 1.04, metatarsus 0.53, tarsus 0.39. Second patella and tibia 0.98 mm, third 0.82. Fourth femur 1.01, patella and tibia 1.04.

Note. The male is considered to be Archer's *X. arawak*, because of the collecting locality and its shape of the abdomen and wide lobe bearing lateral eyes (Fig. 290).

Diagnosis. The female differs from *X. superior,* which also has a wide abdomen, by occurring in the West Indies and Yucatan Peninsula. The male differs from others by the relatively wide abdomen and sickle-shaped paramedian apophysis (on center of Fig. 291).

Specimens Examined. MEXICO *Quintana Roo:* Reserva de Sian Ka'an, S of Felipe Carrillo Puerto, 6 July 1993, 1♂ (G. Alayón, MCZ).

Gasteracantha Sundevall

Gasteracantha Sundevall, 1833: 14. The type species is *Gasteracantha cancriformis.* The gender of the name is feminine (Bonnet, 1957: 1934).

Bunocrania Thorell, 1878: 25. The type species is *B. biloba* from Burma. NEW SYNONYMY.

Vibradellus Chamberlin, 1925: 214. The type species by original designation and monotypy is *V. carolinus* (=*Gasteracantha cancriformis*).

Note. The immature male holotype of *Bunocrania biloba* is in the MCSNG (examined). It matches a mature male collected later (Thorell, 1898: 374), also in the MCSNG, examined. A male determined by Thorell is also in the NRMS (Scharff, personal communication).

More information on the *Gasteracantha* type species designation is found in Levi (1978), and additional information on the numerous *Gasteracantha* synonyms is in Roewer (1942: 935) and Bonnet (1957: 1934).

Diagnosis. The female carapace is square (Fig. 294), high anteriorly (Fig. 293), and reborder ed as in *Micrathena* (Levi, 1985, figs. 18, 19). Unlike species of similar genera, females have a sclerotized hump between epigynum and spinnerets (Levi, 1978, figs. 71, 73). The male carapace is narrow anteriorly (Fig. 308), unlike that of *Encyosaccus,* and the palpus has a circular paramedian apophysis (PM in Fig. 312). In both male and female, the abdomen is wider than long (Figs. 298, 309, 311); in the male, it tends to be widest posteriorly with two posterior, lateral corners (Fig. 311) or posterior–facing, lateral lobes.

Distribution. There are numerous tropical species worldwide but in the Americas only one variable species. A second species may owe its record to an error in curating. Perhaps the competition of the numerous *Micrathena* species, absent from other continents, prevents *Gasteracantha* from speciating.

Relationship. Gasteracantha shares the elongate fourth femur (fourth longer than first) with *Micrathena, Pronous, Hypognatha, Encyosaccus,* and *Xylethrus* (Table 1).

Gasteracantha cancriformis (Linné)
Figures 292–312

Aranea cancriformis Linné, 1767: 1037. Specimens described from America, probably lost.

Aranea tetracantha Linné, 1767: 1037. Specimens from St. Thomas [Virgin Islands], probably lost. Pallas, 1772: 49, pl. 3, figs. 16, 17, ♀. NEW SYNONYMY.

Aranea hexacantha Fabricius, 1787: 344. Named and described without locality.

Epeira lata Walckenaer, 1805: 66. No locality cited, but in 1841: 165, cited as coming from Guadeloupe [Lesser Antilles], specimens lost. NEW SYNONYMY.

Epeira servillei Guérin-Méneville, 1825: 263. Specimens from Brazil. NEW SYNONYMY.

Gasteracantha cancriformis:—Sundevall, 1833: 14.

Acrosoma hexacantha Hahn, 1834: 17, pl. 106, ♀. Specimen from Brazil. NEW SYNONYMY.

Gasteracantha hexacantha:—C. L. Koch, 1838: 31, pl. 268, ♀. Female from Brazil.

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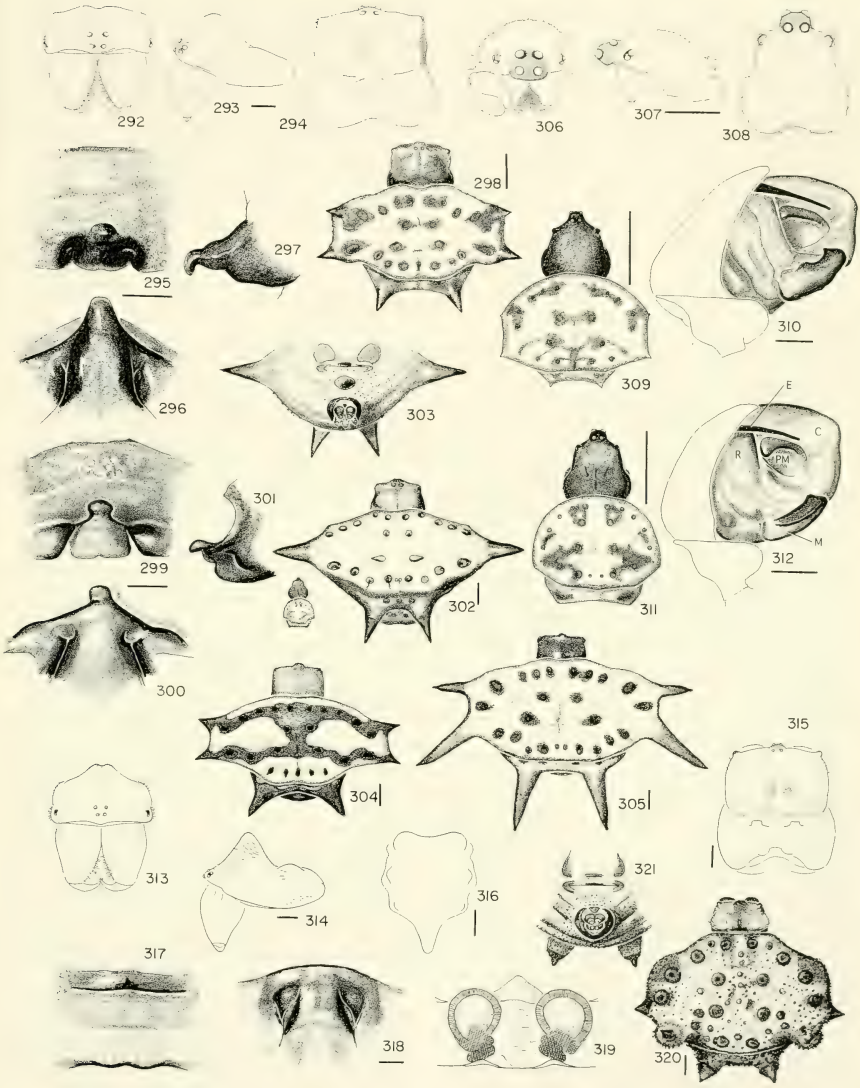
Figures 292–312. *Gasteracantha cancriformis* (Linn.). 292–303, female. 292, eye region and chelicerae. 293, carapace and chelicera, lateral. 294, carapace, dorsal. 295–297, 299–301, epigynum. 295, 299, ventral. 296, 300, posterior. 297, 301, lateral. 298, 302, 304, 305, dorsal. 302, with male. 303, ventral. 306–312, male. 306, eye region, chelicerae and right palpus. 307, carapace and chelicera, lateral. 308, carapace. 309, 311, dorsal. 310, 312, left male palpus. 292–294, 299–303, 306–308, 311, 312, (from Puerto Rico). 295–298, 309, 310, (from Las Lomas, Peru). 304, (from Galapagos Islands). 305, (from Baja California Sur, Mexico).

Figures 313–321. *G. camerunensis* Thorell, female. 313, eye region, chelicerae. 314, carapace, chelicerae, lateral. 315, carapace. 316, sternum. 317–319, epigynum. 317, ventral. 318, posterior. 319, dorsal, cleared. 320, dorsal. 321, abdomen, ventral.



Abbreviations. C, conductor. E, embolus. M, median apophysis. PM, paramedian apophysis. R, radix.

Scale lines. 1.0 mm; except Figures 292–294, 306–308, 313–316, 0.5 mm; genitalia, 0.1 mm.

Gasteracantha velitaris C. L. Koch, 1838: 33, pl. 269, ♀. Female from Brazil.

Gasteracantha elipsoides Walckenaer, 1841: 155. Name applied to Abbot's illustrations of the Insects of Georgia, photocopy examined.

Gasteracantha quinqueserrata Walckenaer, 1841: 157. Female from Guyana, lost.

Gasteracantha sexserrata Walckenaer, 1841: 157. Female from Cayenne [French Guyana], lost.

Plectana triserrata Walckenaer, 1841: 158. Specimens from Guyana and Surinam, lost. NEW SYNONYMY.

Plectana atlantica Walckenaer, 1841: 167. Female from Santa Domingo [Dominican Republic], lost.

Gasteracantha rubiginosa C. L. Koch, 1845: 55, pl. 878. Female from Santa Domingo [Dominican Republic].

Gasteracantha quadridens C. L. Koch, 1845: 59, pl. 880, ♀. Female from St. Thomas, West Indies. NEW SYNONYMY.

Gasteracantha pallida C. L. Koch, 1845: 60, pl. 881, ♀. Specimens from unknown locality. NEW SYNONYMY.

Gasteracantha picea C. L. Koch, 1845: 61, pl. 882, ♀. Specimen from Brazil. NEW SYNONYMY.

Epeira cancer Hentz, 1850: 23, pl. 3, fig. 13, ♀. Females from South Carolina and Alabama, destroyed.

Gasteracantha moesta Thorell, 1859: 301. Female from St. Barthélemy, French Lesser Antilles. NEW SYNONYMY.

Gasteracantha hilaris Thorell, 1859: 302. Female from St. Barthélemy, French Lesser Antilles. NEW SYNONYMY.

Gasteracantha insulana Thorell, 1859: 302. Female from Galapagos Islands in NRMS, examined. NEW SYNONYMY.

Gasteracantha columbiae Giebel, 1863: 312. Black female from Colombia in Giebel Collection (Halle, Saale, Germany), lost.

Gasteracantha kochii Butler, 1873: 169. New name for *Gasteracantha hexacantha:*—C. L. Koch, 1838: 117, fig. 288. Female from Pará [Belém], Brazil. NEW SYNONYMY.

Gasteracantha oldendorffi Holmberg, 1876: 143. Female from Norte del Río Guayquiraró [Prov. Corrientes], Argentina, destroyed.

Gasteracantha callida O. P.-Cambridge, 1879: 284, pl. 26, fig. 7, ♀. Female holotype from Trinidad, West Indies, in HECO.

Gasteracantha raimondii Taczanowski, 1879: 106, pl. 1, figs. 25, 26, ♀. Female syntypes from Lima, Chorillos, and Montana de Nancha, Peru, in PAN, examined.

Gasteracantha raimondii unicolor Taczanowski, 1879: 107. Two females from Lima, Peru, in PAN.

Gasteracantha proboscidea Taczanowski, 1879: 108, pl. 1, fig. 27, ♂. Two male syntypes from Lima, Peru, in PAN, examined.

Gasteracantha rufospinosa Marx, 1883: 25, figs. a–f, ♀, ♂. Female and male from Crescent River, Florida [locality questionable], in USNM, lost.

Gasteracantha elliptica Gétaz, 1893: 105. Females from near San José, Costa Rica, lost.

Gasteracantha maura McCook, 1894: 210, pl. 13, fig. 12, ♀. Syntypes from California, lost.

Gasteracantha preciosa McCook, 1894, p. 211, pl. 14, fig. 7, ♀. Female holotype from "Mohave Desert, Ca", but probably comes from Puerto Rico, in USNM, examined. NEW SYNONYMY.

Gasteracantha biolleyi Banks, 1905: 20, fig. 3, ♀. Female from Cocos Island [Costa Rica], in MCZ, examined.

Gasteracantha kochii var. *joinvillensis* Strand, 1915: 118. Two female syntypes from Joinville, St. Catharina [Est. Santa Catarina], Brazil, in SMF. NEW SYNONYMY.

Gasteracantha mascula Strand, 1915: 119. Male from Haitien, Haiti, in SMF, examined. NEW SYNONYMY.

Gasteracantha comstocki Mello-Leitão, 1917: 91. Female from Goiás and Belo Horizonte [Est. Minas Gerais, Brazil], lost. NEW SYNONYMY.

Vibradellus carolinus Chamberlin, 1925: 214. Male holotype from South Carolina in MCZ, examined.

Gasteracantha tetracantha:—Petrunkevitch, 1930: 253, figs. 104–107, ♀, ♂. Roewer, 1942: 950. Bonnet, 1957: 1970.

Gasteracantha cancriformis:—Roewer, 1942: 949. Bonnet, 1957: 1945. Levi, 1978: 437, figs. 69–85, ♀, ♂.

Note. No attempt was made to examine all the type specimens.

Description. Female from Depto. Las Lomas, Peru (CAS). Eyes subequal. Anterior median eyes about their diameter apart. Posterior median eyes about their diameter apart. Ocular quadrangle about square. Height of clypeus equals to 0.7 diameter of anterior median eye. Total length 4.3 mm. Carapace 2.2 mm long, 2.1 wide in thoracic region, 1.8 wide in eye region. First femur 1.7 mm, patella and tibia 1.7, metatarsus 1.0, tarsus 0.4. Second patella and tibia 1.6 mm, third 1.1. Fourth femur 2.1 mm, patella and tibia 1.7, metatarsus 1.1, tarsus 0.4.

Male from Depto. Las Lomas, Peru (CAS). Posterior median and lateral eyes 0.8 diameter of anterior medians. Anterior median eyes 0.8 diameter apart. Posterior median eyes 1 diameter apart. Median ocular quadrangle slightly wider in front than behind. Endite without tooth. Palpal patella without macroseta. First coxa without

hook. Abdomen as in female. Total length 2.4 mm. Carapace 1.18 mm long, 0.96 wide in thoracic region, 0.73 wide in eye region. First femur 0.78 mm, patella and tibia 0.85, metatarsus 0.46, tarsus 0.36. Second patella and tibia 0.66 mm, third 0.47. Fourth femur 0.75 mm, patella and tibia 0.68, metatarsus 0.39, tarsus 0.32.

Variation. Specimens come in various colors, white, yellow, orange, red, or sometimes all black with black patches on light (Fig. 298) or bands (Fig. 304) on the abdomen. The most distinctive are specimens from Puerto Rico and some of the Antilles that have only four spines (Figs. 302, 303), having lost the most anterior pair. But specimens from Bahamas and Hispaniola that look like the specimens from Puerto Rico have a minute to small anterior pair of spines. North American males have a body that resembles the male from Puerto Rico (Fig. 311); South American males usually have six points on the abdomen (Fig. 309). (There are only a few males from South America in North American collections, and no attempt was made to borrow specimens from South America.) The variability in color and form of the spines has resulted in a proliferation of names and descriptions and numerous synonyms. Despite the many synonymies, there are intermediates between the forms and the genitalia show little variation.

Figures 295–298, 309, and 310 were made from specimens from Higuerón, Las Lomas [Depto. Piura], Peru (CAS), Figures 292–294, 299–303, 306–308, 311, and 312 from specimens from Jayuya, Puerto Rico (MCZ), Figure 304 from a specimen from Galapagos Islands (MCZ), and Figure 305 from Desierto del Vixcaino, La Bocana, Baja California Sur, Mexico (MLJ, MCZ).

Diagnosis. The shape of the body with three (or sometimes six) spines (Figs. 298, 302, 304, 305) and the shape of the male body (Figs. 309, 311) separate *G. cancriformis* from all other American orb weavers. The female is separated from other female *Gasteracantha* species by its epigynum with a median posterior knob in ventral view (Figs. 295, 299) and posteriorly a subtriangular median plate separated dorsally and coming to, almost joining, at the knob ventrally (Figs. 296, 300). The male is separated by its palpus with an almost circular paramedian apophysis (Fig. 310, PM in Fig. 312), median apophysis with a distal knob (M in Fig. 312), the even slope of the embolus (Fig. 310, E in Fig. 312), and a transparent conductor (C in Fig. 312).

Distribution. This is one of the most common tropical and subtropical American spiders occurring in the north from North Carolina to Oklahoma and southern California (Levi, 1978). The most southern records (in North American collections) are from Paraguay and from Tucuman, Argentina. No attempt was made to get the southernmost collections. The species also occurs in Hawaii and on the Galapagos Islands. It is found in semiarid or dry habitats, not in dark, wet forests.

Gasteracantha camerunensis Thorell
Figures 313–321

Gasteracantha camerunensis Thorell, 1899: 65. Female holotype from Cameroon, lost (N. Scharff, personal communication).

Gasteracantha brevispina camerunensis:—Bonnet, 1957: 1945.

Gasteracantha batesi:—Roewer, 1942: 935.

Description. Female from Venezuela. Carapace dark orange to black with white setae on each side. Chelicerae orange-brown. Labium, endites, sternum orange to brown. Coxae, legs orange, third and fourth with brown rings. Abdomen light orange with black patches and some anterior median white pigment spots dorsally (Fig. 320). Carapace with cephalic region high (Figs. 313–315). Sternum with humps at first and second coxae and with median posterior projection (Fig. 316). Eyes subequal in size. Anterior median eyes 1 diameter apart. Posterior median eyes 1.7 diameters apart. Ocular quadrangle wider behind than in front. Abdomen with three

pairs of large spines (Fig. 320). Total length 9.0 mm. Carapace 3.4 mm long, 3.2 wide in thoracic region, 2.6 wide behind posterior eyes, 2.9 widest in cephalic region. First femur 2.3 mm, patella and tibia 2.6, metatarsus 1.3, tarsus 0.9. Second patella and tibia 2.5 mm, third 1.5, fourth 2.5. Abdomen 6.9 mm long, 9.5 wide.

Note. We assume that the single specimen found, a rare African species, represents an error of labeling locality. The rarity of this species in Africa and the remoteness of the Venezuelan locality where it was allegedly found make it unlikely that this is an introduced species.

Specimen Examined. VENEZUELA *Amazonas:* Rio Bario [Río Baria], betw. Pico de Neblina and San Carlos, Venezuela, 7–9 May 1984, 1 ♀ (J. Cracraft, AMNH).

Enacrosoma Mello-Leitão

Enacrosoma Mello-Leitão, 1932: 78. Type species *Epeira anomala* Taczanowski, by original designation. Neave, 1939b: 733. The generic name is neuter (Bonnet, 1956: 1654).

Note. Simon (1884) established the genus *Glyptogona* and made the Mediterranean *Epeira sextuberculata* Keyserling the type species. Later, Simon (1895b: 867) redescribed the genus but illustrated the description with the dorsal view of the American *Glyptogona sexlobata* Simon (=*E. anomalum*), a different species, but again listed *G. sextuberculata* Keyserling as the type species.

Mello-Leitão (1932), when establishing the genus *Enacrosoma,* made *Epeira anomala* the type species and also placed *Acrosoma quadrituberculatum* Simon in the genus. Both species had been placed in the genus *Micrathena* by Simon (1895b: 862).

Did Simon misidentify the Mediterranean Keyserling species? It is certain that this was not the case, as determined female and male specimens of the Keyserling species were loaned to me from the Paris museum, and Keyserling's (1863) illustrations of the epigynum and abdomen of this species match those of the determined specimens. The catalogs of both Roewer (1942) and Bonnet (1957) kept most American species in *Glyptogona. Glyptogona* is illustrated with Figures 360–363.

Diagnosis. The abdomen is wider than long, with about five pairs of lateral humps and sclerotized spots (Figs. 329, 330, 338, 342, 343, 357). The spots may be tiny tubercles, each bearing a seta, distinguishing *Enacrosoma* from most other araneid genera including *Colphepeira* Archer (Levi, 1978). Endites, labium, sternum, and legs are tuberculate. The female (but not male) has the fourth femur as long or longer than the first, but in total length the first leg exceeds the fourth. The sternum, as in *Xylethrus,* has the posterior end truncate (Fig. 325), sometimes hidden by tubercles. The female differs from those of *Encyosaccus, Xylethrus,* and *Gasteracantha,* which also have the fourth femur longer than the first, by the shape of the abdomen, by the small size, and by having the cephalic region of the carapace narrower than the thoracic region (Figs. 324, 333).

The male differs from those of other genera by the shape of the abdomen (Fig. 338), which is similar to that of the female (Fig. 330). The male of *Enacrosoma* (also *Colphepeira* and *Glyptogona*) differs from males of other genera by being only slightly smaller than the female (Figs. 330, 338) and by the narrow cephalic region (Figs. 324, 333) and having the first femur longer than fourth. As in other araneid genera in which the female is only slightly larger, the male has a tooth on the endite (ET in Fig. 331), a hook on the first coxa (CXH in Fig. 331), and a tiny groove on the second femur (GR in Fig. 334), but both hook and matching groove are small.

Description. Small spiders, less than 5 mm total length. Coloration white and orange with patches of brown and black. Thoracic region of carapace usually brown. Clypeus light. Chelicerae, and sternum with brown patches, sternum with brown margin. Legs orange with brown rings. Dorsum of abdomen with paired, indis-

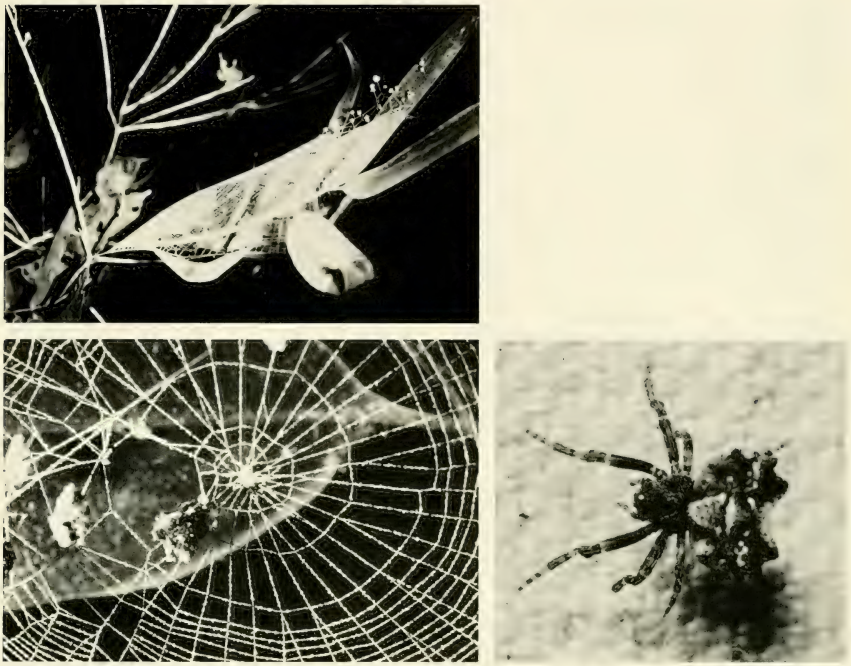


Plate 2. Upper, web of *Enacrosoma anomalum*, from Madre de Dios Dept., Peru, diameter unknown. Lower left, close up of web, spider among debris, spider about 3 mm total length (photos D. Silva D.). Lower right, female *E. frenca*, from Chiapas State, Mexico, total length about 3 mm (photo W. Maddison).

tinct, darker patches and darker spots (Fig. 330, 343, 349, 357); venter without distinct pattern. Carapace with scattered, short, white setae.

Posterior median eyes slightly smaller than anterior medians, diameter of laterals 0.5 to 0.7 diameter of anterior median eyes. Anterior median eyes 0.5 to 0.8 their diameter apart, 1 to 1.8 diameters from laterals. Posterior median eyes 0.8 to 1.5 diameters apart, 1.8 to 3 diameters from laterals. Ocular trapezoid almost square, slightly narrower behind than in front (Figs. 324, 333). Height of clypeus equals 0.8 to 1 diameter of anterior median eye (Figs. 322, 331). Carapace with fine tubercular texture. Endites, labium, sternum tubercular. Proximal leg articles tubercular. First and second femora with three to eight median ventral tubercles in a row that form bases for short setae (Fig. 334).

Abdomen wider than long, with about five pairs of humps, additional smaller humps, and sclerotized spots (Figs. 329, 330, 342, 343, 356, 357). A sclerotized ring around spinnerets (Fig. 326), its proximal edge indistinct. Ring with two lobes at 4 and 8 hr of circle (Fig. 326). The male is like the female and not much smaller.

Genitalia. Epigynum with a median lobe tipped by a median secondary lobe (Figs. 327, 328, 339, 340).

Palpus with conductor in middle of tegulum (C in Figs. 336, 345), with an ex-

tension that probably is a paramedian apophysis (PM in Figs. 336, 345), most distinct as a round structure in *E. anomalum.* Large median apophysis (M in Figs. 336, 345) and a terminal apophysis (A in Figs. 336, 337, 345). Embolus and terminal apophysis may be complex structures (Figs. 336, 337). Palpal patella with only one weak macroseta.

Natural History. The orbweb is close to horizontal, tightly meshed with the spider resting during the day in a retreat made of bits of debris and plant parts, at the edge of the web (Pl. 2). A retreat of *E. javium,* kept with the specimen, is 10–15 mm long but may have been torn during collecting. Attached between and on the debris are numerous early instar spiderlings. An eggsac of *E. multilobatum* was 5 mm long, about 8 mm wide, and was covered with debris, as was the retreat. The spiders occur in secondary forest and may be common (in Colombia, W. Eberhard, letter Oct. 1990). Some spiders were collected at night in Peru, one by fogging vegetation.

Relationship. The elongate fourth femur of the female is probably a synapomorphy of *Encyosaccus, Hypognatha,* and other genera belonging to the *Gasteracantha* group of genera. The similar size of male and female and the palpus resembling those of *Alpaida* and *Wagneriana* are probably plesiomorphic features.

Enacrosoma is probably not close to *Glyptogona. Glyptogona,* described from Syria and fairly common in southeastern Europe, has an annulated scape of the epigynum (Figs. 359, 360), and the male has a large round terminal apophysis, facing the mesal surface of the palpus (A in Figs. 364, 365).

Distribution. There are only six species, all American; four of the six species are Central American (Map 5).

Misplaced Species. Nicolet (1849) named species in *Gasteracantha* that have been placed in *Glyptogona* together with the species here placed in *Enacrosoma.* All Nicolet's species seem to belong in *Phoroncidia* (Theridiidae). Simon (1894: 556) placed *Gasteracantha scutata, G. gayi,* and *G. pennata* in *Ulesanis* (=*Phoroncidia*) but later in the same volume (1895b: 867) referred to them in *Glyptogona.* Sedgwick (1973: 354) found specimens of two Nicolet species, *G. pennata* and *G. variabilis,* and placed them in *Phoroncidia.* Others are *Gasteracantha fumosa, G. pallida, G. spissa,* and *G. umbrosa,* all here placed in *Phoroncidia* (NEW COMBINATIONS). A specimen of *Gasteracantha fumosa* was examined. Roewer (1942: 691) replaced the name *G. pallida* Nicolet, a homonym of *G. pallida,* C. L. Koch, 1845, with *nicoleti.*

Simon described *Acrosoma quadrituberculatum* (1876: lxxxviii) and later placed it in *Micrathena* (1895b: 862). Mello-Leitão (1932: 75, 77) placed the species in *Enacrosoma.* In the catalogs (Roewer, 1942; Bonnet, 1957), it appears in *Enacrosoma,* although the type is lost (in the museum in Troyes, France), and nobody knows what the species is.

KEY TO FEMALE *ENACROSOMA*

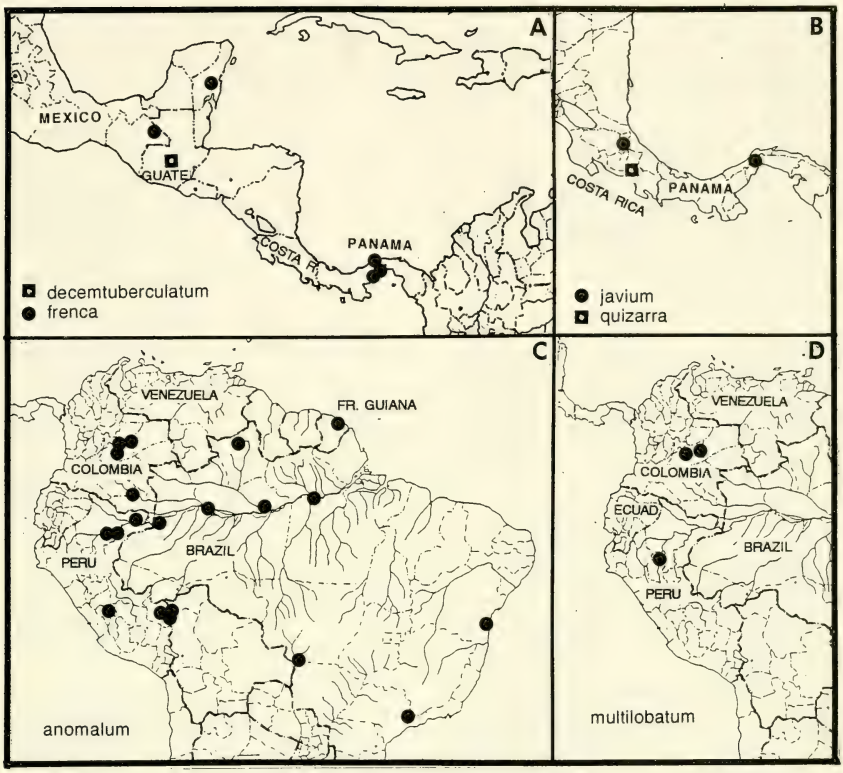
Female of *E. decemtuberculatum* is not known.

1. Female from South America (Maps 5C, D) 2
– Female from Central America (Maps 5A, B) 3

2(1). Humps of the abdomen spherical (Figs. 356, 357); sclerotized epigynum about as wide as long (Figs. 354, 355); total length 4–5 mm ..... *multilobatum*
– Humps conical, pointed (Figs. 342, 343); epigynum wider than long (Figs. 339, 340); total length 2.5–3.5 mm ..... *anomalum*

3(1). Thoracic region of carapace with a light V-shaped mark (Fig. 330); median plate of epigynum, in posterior view, with almost parallel sides (Fig. 328) ..... *frenca*
– Thoracic region of carapace marked otherwise (Figs. 349, 353); median plate of epigynum narrower dorsally than ventrally (Figs. 347, 351) 4

4(3). Thoracic region of carapace light in median area (Figs. 349); epigynum wider than long (Figs. 346, 347) ..... *javium*
– Thoracic region of carapace with four indistinct, light patches (Fig. 353); epigynum longer than wide (Figs. 350, 351) ..... *quizarra*



Map 5. Distribution of *Enacrosoma* species.

KEY TO *ENACROSOMA* MALES

The males of *E. javium*, *E. multilobatum*, and *E. quizarra* are not known.

1. Carapace with light V-shaped mark (Fig. 338); embolus consisting of two claw-shaped structures (Fig. 335, E, d in Fig. 336); Central America (Map 5A) ..... *frenca*
– Carapace marked otherwise; embolus otherwise 2
2(1). A black pointed portion of terminal apophysis behind a more transparent section (Fig. 344, A in Fig. 345); median apophysis almost square (Fig. 344, M in Fig. 345); South America (Map 5C) *anomalum*
– Terminal apophysis otherwise (Fig. 358); median apophysis otherwise (Fig. 358); Guatemala (Map 5A) ... *decemtuberculatum*

Enacrosoma frenca new species
Figures 322–338; Map 5A

Holotype. Female holotype, one female, two male, and one immature paratypes from France Field, Canal Zone [Colón Prov.], Panama, Aug. 1939 (A. M. Chickering), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Total length 2.7 mm. Carapace 1.10 mm long, 1.05 wide in thoracic region, 0.63 wide in cephalic region. First femur 1.00 mm, pa-

tella and tibia 1.17, metatarsus 0.49, tarsus 0.37. Second patella and tibia 1.07 mm, third 0.65. Fourth femur 1.00, patella and tibia 0.91, metatarsus 0.45, tarsus 0.37.

Male paratype. Second tibia as thick as first. Total length 1.8 mm. Carapace 1.14 mm long, 0.99 wide in thoracic region, 0.56 wide in cephalic region. First femur 0.90 mm, patella and tibia 1.07, metatarsus 0.46, tarsus 0.36. Second patella and tibia 0.94 mm, third 0.61. Fourth femur 0.83 mm, patella and tibia 0.74, metatarsus 0.39, tarsus 0.27.

Note. Males and females were collected together.

Variation. Total length of females 2.3 to 3.1 mm, males 1.8 to 2.2 mm. The illustrations were made from the female holotype and male paratype.

Diagnosis. Enacrosoma frenca differs from other species by the distinct light V-shaped mark on the the thoracic region of the carapace (Figs. 330, 338). The epigynum has a secondary median lobe that is longer than wide (Fig. 327), whereas that of *E. anomalum* is wider than long (Fig. 339). The embolus of the palpus appears to have a pair of claws (Fig. 335, E in Fig. 336), whereas that of *E. anomalum* is hidden below the terminal apophysis (Fig. 345). The median apophysis of *E. frenca* is elongate (Fig. 335, M in Fig. 336), whereas that of *E. anomalum* is square (Fig. 344, E in Fig. 345). *Enacrosoma frenca* has the most pointed humps on the abdomen.

Natural History. Specimens have been found in roadside bushes of tropical rain forest in Chiapas, Mexico.

Specimens Examined. MEXICO *Quintana Roo:* San Felipe de Bacalar, 8 July 1993, 1♂ (G. Alayón, CIQRO). *Chiapas:* 105 km SE Palanque on road to Bonampak, 8, 9 July 1983, 1♀ (W. Maddison, MCZ). PANAMA *Panamá:* Arraiján, July 1950, 1♀ (A. M. Chickering, MCZ); Barro Colorado Island, July 1936, 3♀, 3♂, 1 imm., Aug. 1939, 9♀, 7♂, 15 imm., June 1950, 1♀, 1♂, 1 imm., July 1950, 2♀, 1♂, 2 imm.; Experimental Gardens, July 1954, 1♂; Fort Randolph, 13 Aug. 1936, 1♀, 1 imm.; Fort Sherman, Aug. 1939, 1♀; Summit, July 1950, 1♂ (all A. M. Chickering, MCZ).

Enacrosoma anomalum (Taczanowski) Figures 339–345; Map 5C

Epeira anomala Taczanowski, 1873: 144, pl. 5, fig. 19, ♀. Two female, two male, and an immature syntypes from Cayenne, French Guiana, in PAN, examined.

Inca branickii Taczanowski, 1879: 105. Male paralectotype from Amable María [Depto. Junín], Peru, in PAN, not female lectotype (=*Aspidolasius branicki*).

Gasteracantha anomala:—Taczanowski, 1879: 108.

Xylethrus superbus Simon, 1895b: 895. Male paralectotype from São Paulo [São Paulo de Olivença, Amazonas State], Brazil, in MNHN, not female lectotype.

Micrathena anomala:—Simon, 1895b: 862.

Glyptogona sexlobata Simon, 1895a: 160. Female holotype from Pebas [Depto. Loreto], Peru, in MNHN, examined. Roewer, 1942: 891. Bonnet, 1957: 1999. NEW SYNONYMY.

Glyptogona leprosa Simon, 1897: 471. Male holotype

→

Figures 322–338. *Enacrosoma frenca* n. sp. 322–330, female. 322, eye region and chelicerae. 323, carapace and chelicera, lateral. 324, carapace. 325, sternum and labium. 326, spinnerets. 327, 328, epigynum. 327, ventral. 328, posterior. 329, abdomen, lateral. 330, dorsal. 331–338, male. 331, eye region, chelicerae and right palpus. 332, carapace and chelicera, lateral. 333, carapace, dorsal. 334, second left leg from anterior. 335–337, left palpus. 335, mesal. 336, 337, expanded. 336, mesal. 337, embolus and terminal apophysis, dorsal. 338, dorsal.

Figures 339–345. *E. anomalum* (Taczanowski). 339–343, female. 339–341, epigynum. 339, ventral. 340, posterior. 341, posterior, cleared. 342, abdomen, lateral. 343, dorsal. 344, 345, male palpus. 344, mesal. 345, mesal, expanded.

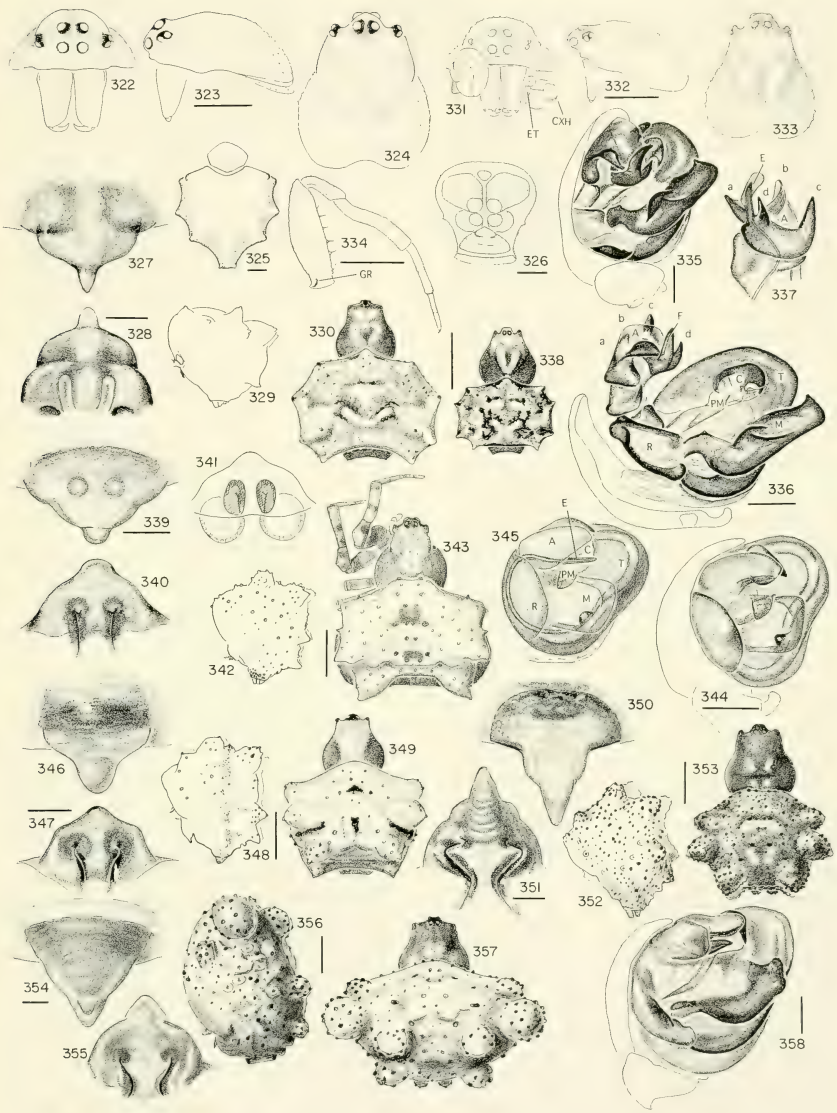
Figures 346–349. *E. javium* n. sp., female. 346, 347, epigynum. 346, ventral. 347, posterior. 348, abdomen, lateral. 349, dorsal.

Figures 350–353. *E. quizarra* n. sp., female. 350, 351, epigynum. 350, ventral. 351, posterior. 352, abdomen, lateral. 353, dorsal.

Figures 354–357. *E. multilobatum* (Simon), female. 354, 355, epigynum. 354, ventral. 355, posterior. 356, abdomen, lateral. 357, dorsal.

Figure 358. *E. decemtuberculatum.* (O. P.-Cambridge). male. 358, palpus.

Abbreviations. A, terminal apophysis. C, conductor. CXH, coxal hook. E, embolus. ET, endite tooth. GR, groove. M, median apophysis. PM, paramedian apophysis. R, radix. T, tegulum. a. b, c, d letters to compare position of Figures 336, 337.



Scale lines. 1.0 mm; except Figures 322–324, 331–334, 0.5 mm; Figures 325, 326 and genitalia 0.1 mm.

from Venezuela in MNHN, examined. Roewer, 1942: 891. Bonnet, 1957: 1999. NEW SYNONYMY.

Enacrosoma anomalum:—Mello-Leitão, 1932: 78. Roewer, 1942: 952. Bonnet, 1956: 1654.

Description. Female from Santarém. Carapace orange, sides of thoracic region brown. Abdomen white, black, gray on colorless background, without well-defined spots (Fig. 346). Venter of abdomen mostly white spots with some black. Total length 3.3 mm. Carapace 1.43 mm long, 1.22 wide in thoracic region, 0.78 wide in cephalic region. First femur 1.23 mm, patella and tibia 1.40, metatarsus 0.60, tarsus 0.44. Second patella and tibia 1.24 mm, third 0.87. Fourth femur 1.30 mm, patella and tibia 1.17, metatarsus 0.52, tarsus 0.42.

Male from Santarém. Total length 1.9 mm. Carapace 1.04 mm long, 0.92 wide in thoracic region, 0.49 wide in cephalic region. First femur 1.01 mm, patella and tibia 1.09, metatarsus 0.47, tarsus 0.36. Second patella and tibia 0.91 mm, third 0.74. Fourth femur 0.91 mm, patella and tibia 0.83, metatarsus 0.39, tarsus 0.30.

Note. Males and females were collected together.

Variation. Total length of females 2.6 to 3.7 mm, males 1.8 to 2.5. The illustrations were made from a female from Santarém (Figs. 339–342), a syntype (Fig. 343), and a male from Santarém (Figs. 344, 345).

Diagnosis. The sclerotized part of the epigynum is wider than long and the small distal lobe, unlike that of *E. frenca* (Fig. 327), is wider than long (Fig. 339), and the posterior median plate has sides that are almost parallel (Fig. 340). The male differs by having a sclerotized lobe in the palpus whose distal tip is visible under the terminal apophysis (Fig. 344, A in Fig. 345) and a median apophysis (Fig. 344; M in Fig. 345) which is almost square.

Natural History. Specimens were collected in forest in Santarém.

Specimens Examined. COLOMBIA *Meta:* Lomalinda nr. Puerto Lleras, 3°18′N, 73°22′W, Sept. 1987, 1♀, 1♂, Nov. 1987, 1♀, 3 imm. (B. T. Carroll, CAS); 15 km SW Puerto Lopez, 200 m, Aug. 1978, 1♀ (W. Eberhard, MCZ); Carimagua, 20 km N Río Muco, no date, 2♀, Oct. 1973, 3♀ (W. Eberhard, MCZ). *Amazonas:* Araracuara, 270 m, 16 Mar. 1988, 1♀ (C. Valderrama, CV). PERU *Loreto:* Cocha San Martín, Río Samiria, fogging, 8 May 1990, 1♀ (D. Silva D., MUSM), fogging, 20 May 1990, 1♂ (T. Erwin, D. Silva D., MUSM); Genaro Herrera, 04°55′S, 73°45′W, 1♀ (D. Silva D., MUSM). *Junín:* Amable María, 1♀ (Taczanowski coll., PAN). *Madre de Dios:* Albergue Cuzco Amazonico, 12°33′S, 69°03′W, 12 June 1989, 1♀, 1 July 1989, 1♀, 23 Feb. 1990, 1♀, 4 imm., 8 Mar. 1990, 1♀ (D. Silva D., MUSM); Zona Reservada Tambopata, 12°50′S, 69°17′W, 20, 22 July 1987, 2♀ (D. Silva D., MUSM); Zona Reservada Pakitza, 25 Apr. 1991, 1♀, 1 imm, 7 May 1991, 1♀, 13 May 1991, 2♀, 6 Oct. 1991, 1♂ (D. Silva D, MUSM). BRAZIL *Pará:* Santarém, 1♀, 1♂ (BMNH 97.9.20.260–72). *Roraima:* Maracá, 24 Mar. 1987, 1♀ (A. A. Lise, INPA); Ilha de Maracá, 4 Dec. 1987, 1♂ (A. A. Lise, INPA), 31 Jan.–24 Feb. 1992, 3♀, 3♂, 7 imm. (A. B. Bonaldo, MCP 1886); Ilha de Maracá, Rio Uraricoera, 21 Mar. 1987, 1♀ (A. A. Lise, MCN 25560); 8 Dec. 1987, 1♀ (E. H. Buckup, MCN 25561). *Amazonas:* Manaus, 14 Mar. 1987, 1♀, 1♂ (A. A. Lise, MCN 25567); Estação Ecológica de Mimirauá, Tefé, 9–13 Oct. 1993, 1♀ (S. H. Borges, MCN 22965). *Bahia:* Fazenda Almada Uruçuca, 26 Nov. 1977, 1♂ (J. S. Santas, MCN 10292). *Mato Grosso:* Pantanal, 4–10 Aug. 1992, 1♀, 1♂, 4 imm. (A. A. Lise, G. A. Braul, MCP 2334). *São Paulo:* Capital, Agua Funda, 13 July 1941, 1♂ (B. M. Soares, Brandas, MZSP 7476).

Enacrosoma javium new species
Figures 346–349; Map 5B

Holotype. Female holotype from Finca La Selva, 50 m, near Puerto Viejo, Heredia, Costa Rica, June 1982 (W. Eberhard, no. TL 32–5), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace orange, sides of thoracic region brown, center light (Fig. 349) or with a median brown patch on orange. Total length 3.6 mm. Carapace 1.55 mm long, 1.34 wide in thoracic region, 0.77 wide in cephalic region. First femur 1.40 mm, patella and tibia 1.48, metatarsus 0.70, tarsus 0.44. Second patella and tibia 1.40 mm, third 0.96. Fourth femur 1.41 mm, patella and tibia 1.26, metatarsus 0.65, tarsus 0.42.

Variation. Total length of females 2.6 to 3.6 mm. The illustrations were made from the holotype.

Diagnosis. This species differs from others by having the median thoracic region light (Fig. 349), sometimes with a me-

dian dark patch. The sclerotized region of the epigynum is wider than long, the median distal lobe is as wide as long (Fig. 346), and the distal lobe is relatively larger than that of *E. frenca* (Fig. 327) or *E. anomalum* (Fig. 339). The humps of the abdomen (Fig. 349) are more swollen than those of *E. frenca*.

Paratypes. COSTA RICA *Heredia*: La Selva, nr. Puerto Viejo, Feb. 1981, 1♀ (W. Eberhard, 2197, MCZ).

Specimens Examined. PANAMA *Panamá*: Barro Colorado Island, 9 Mar. 1973, 1♀ (Y. Lubin, H. Levi); Sept. 1975, 1♀, Oct. 1975, 1♀ (W. Eberhard, MCZ).

Enacrosoma quizarra new species
Figures 350–353; Map 5B

Holotype. Female holotype, five female paratypes from near Quizarra, 6 km E San Isidro del General, 750 m, Puntarenas Prov., Costa Rica, May 1989 (W. Eberhard 3537) in MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown, posteriorly with two pairs of light orange patches in median (Fig. 353). Total length 3.8 mm. Carapace 1.86 mm long, 1.56 wide in thoracic region, 1.01 wide in cephalic region. First femur 1.47 mm, patella and tibia 1.70, metatarsus 0.85, tarsus 0.55. Second patella and tibia 1.59 mm, third 1.10. Fourth femur 1.57 mm, patella and tibia 1.46, metatarsus 0.85, tarsus 0.52.

Note. The illustrations were made from the female holotype.

Diagnosis. This species differs from other Central American *Enacrosoma* by having the tubercles of the abdomen more rounded. It differs from all other *Enacrosoma* species by having the sclerotized portion of the epigynum longer than wide (Figs. 350, 351) and the posterior median plate trapezoid in shape, the dorsal width narrower than the ventral width (Fig. 351).

Specimens Examined. COSTA RICA *Puntarenas*: Quizarro, 9.6 km E San Isidro del General, 750 m, 11 Oct. 1981, 1♀ (W. Eberhard FN 3–4A, MCZ).

Enacrosoma multilobatum (Simon) new combination
Figures 354–357; Map 5D

Glyptogona multilobata Simon, 1897: 472. Female holotype from Tarapoto [Depto. San Martín], Peru, in MNHN no. 9729, examined. Roewer, 1942: 891. Bonnet, 1957: 1999.

Description. Female from near El Porvenir, Colombia. Carapace dark brown with several narrow, irregular light lines in middle of thoracic region. Total length 5.0 mm. Carapace 2.2 mm long, 1.9 wide in thoracic region, 1.1 wide in cephalic region. First femur 1.9 mm, patella and tibia 2.1, metatarsus 1.1, tarsus 0.6. Second patella and tibia 2.0 mm, third 1.3. Fourth femur 2.1 mm, patella and tibia 1.8, metatarsus 1.1, tarsus 0.6.

Note. The illustrations were made from female specimens from Colombia.

Diagnosis. This species is larger than the other *Enacrosoma* and has the tubercles of the abdomen almost spherical (Figs. 356, 357). The epigynum is triangular, about as wide as long (Fig. 354), and the posterior median plate is narrower dorsally than ventrally (Fig. 355).

Specimens Examined. COLOMBIA *Meta*: Finca Chenevo, 20 km N Río Muco, 20 km S El Porvenir, 1978, 1♀ (W. Eberhard, MCZ); Hacienda Mozambique, 15 km SW Puerto Lopez, 200 m, Aug. 1978, 1♀ (W. Eberhard, MCZ).

Enacrosoma decemtuberculatum (O. P.-Cambridge) new combination
Figure 358; Map 5A

Cyrtarachne decemtuberculata O. P.-Cambridge, 1889: 59, pl. 4, fig. 4, ♂. Male holotype from Guatemala in BMNH no. 1905.4.28.3222, examined. Keyserling, 1892: 57, pl. 3, fig. 45, ♂.

Glyptogona decemtuberculata:—F. P.-Cambridge, 1904: 523. Roewer, 1942: 891. Bonnet, 1957: 1998.

Description. Male. Carapace dark brown, with a pair of light streaks on posterior slope of thoracic region underneath abdomen. Sternum brown, lighter anterior in center. First femur brown, otherwise ringed brown and yellowish. Abdomen with brown, black, gray spots and patches,

a pigmentless patch between posterior tubercle and spinnerets. Abdomen almost spherical, with setose humps. Total length 3.0 mm. Carapace 1.6 mm long, 1.5 wide in thoracic region, 0.8 wide in cephalic region. First femur 1.4 mm, patella and tibia 1.5, metatarsus 0.8, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.9. Fourth femur 1.3, patella and tibia 1.2, metatarsus 0.8, tarsus 0.5.

Note. This may be the male of *E. quizarra.*

Diagnosis. The shape of the median apophysis, embolus, and terminal apophysis (Fig. 358) separate this species from *E. frenca* and *E. anomalum.*

Glyptogona Simon

Glyptogona Simon, 1884: 326. Type species, designated by Simon, is *Epeira sextuberculata* Keyserling, 1863. The gender of the name is feminine (Bonnet, 1957: 1998).

Diagnosis. Unlike that of other araneids, the abdomen of *Glyptogona* (Fig. 362) is about the same shape as that of *Colphepeira* Archer, 1941 (Levi, 1978, fig. 1) and, as in *Colphepeira,* but unlike that of *Enacrosoma,* it lacks sclerotized spots and sclerotized ring around spinnerets. Unlike both *Colphepeira* and *Enacrosoma,* its clypeus is high, about 2 diameters or more of the anterior median eye. All three genera have tuberculate sternum and coxae. Unlike *Enacrosoma, Glyptogona* and *Colphepeira* have the fourth femur and fourth leg shorter than the first.

The males, in *Colphepeira* and *Enacrosoma,* are only slightly smaller than females. As in *Colphepeira* (Levi, 1978, fig. 9), the epigynum has an annulate scape (Figs. 359–361). The male, as in both other genera, has only one patellar macroseta. The palpus resembles that of *Colphepeira* (Levi, 1978, figs. 12–15, and see below), but the embolus is twisted with the terminal apophysis and is positioned distally from the terminal apophysis (A, E in Figs. 363–365). The similarities between *Colphepeira* and *Glyptogona* were overlooked when I worked on *Colphepeira* (Levi, 1978).

Distribution. Glyptogona sextuberculata is eastern Mediterranean in distribution, and the only other species in the genus is *G. duriuscula* Simon (not examined) from Sri Lanka.

Glyptogona sextuberculata (Keyserling) Figures 359–365

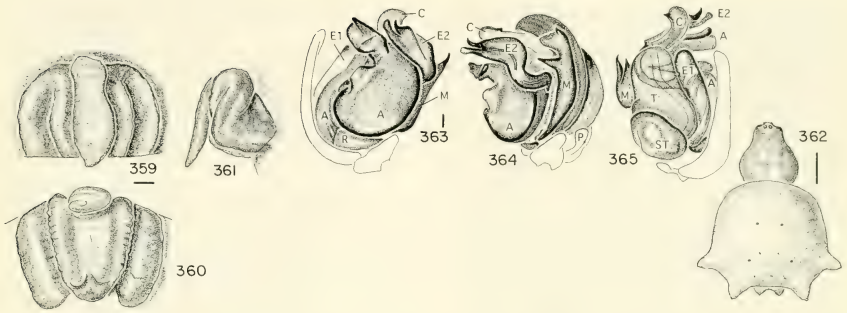
Epeira sextuberculata Keyserling, 1863: 381, pl. 10, ♀. Female holotype from Dalmatia, not examined.
Glyptogona sextuberculata:—Simon, 1884: 326; 1895b: 867. Roewer, 1942: 891. Bonnet, 1957: 1999. Levy, 1985: 50, fig., ♀.

Note. The genitalia have not been illustrated since Keyserling's original description of a female. Levy (1985) has a color photograph of a female.

Description. Female. Height of clypeus equals 2 diameters of anterior median eye. Sternum, coxae tubercular. Sternum pointed. Small row of tubercles along venter of first femur. Total length 5.5 mm.

Male. Height of clypeus equals 2.5 diameters of anterior median eye. Large endite tooth and hook on first coxa with matching groove on second femur. First femur with ventral tubercles. Leg lengths 1, 2, 4, 3. First tibia with many macrosetae on anterior, few on second. Total length 4.4 mm.

Genitalia. The conductor of the male palpus sits on the margin of the tegulum in the male palpus (C in Figs. 363–365) and has a distal tooth (also in *Colphepeira*); the median apophysis (M in Fig. 364) has large spines resembling those of the *Araneus* palpus. The embolus and terminal apophysis are complex structures and are twisted so the embolus seems to originate as a branch from the terminal apophysis, rather than the reverse. The embolus originates from the most proximal end of the terminal apophysis, close to the radix (R in Fig. 363) and is an upright post (E1 in Fig. 365), having a distal transverse spine and more proximally a transverse stalk (both spine and stalk are hidden by



Figures 359–365. *Glyptogona sextuberculata* (Keyserling) (from the eastern Mediterranean region). 359–362, female. 359–361, epigynum. 359, ventral. 360, posterior. 361, lateral. 362, dorsal. 363–365, male, left palpus. 363, mesal. 364, ventral. 365, dorsal.

Abbreviations. A, terminal apophysis; C, conductor; E1, E2, embolus.; M, median apophysis; P, paracymbium; R, radix; T, tegulum; ST, subtegulum.

Scale lines. 1.0 mm; genitalia 0.1 mm.

the tegulum, T in Fig. 365). Distally, the stalk emerges, expands, and forms a visible part of the embolus (E2 in Figs. 363, 364). The terminal apophysis is a complex structure whose surface is a large disk, which is visible in mesal view (A in Fig. 363). The palpus has no paramedian apophysis.

Note. The illustrations were made from specimens from Lebanon in the MNHN, redrawn with the help of specimens from Croatia in the MCZ collection. Figure 365 was drawn from a Croatian male.

Natural History. One female in Israel was found under a stone, another among leaves on the ground, close to a tree trunk. The spiders did not have a web and would not build in the laboratory (G. Levy, personal communication).

Distribution. Southeastern Europe, Lebanon, and Israel.

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RICHARD I. JOHNSON

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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TYPES OF LAND AND FRESHWATER MOLLUSKS FROM THE HAWAIIAN ISLANDS IN THE MUSEUM OF COMPARATIVE ZOOLOGY

RICHARD I. JOHNSON[1]

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ABSTRACT. Types of Hawaiian land and freshwater mollusks described by C. B. Adams, C.-M. F. Ancey, D. D. Baldwin, T. D. A. Cockerell, C. M. Cooke, Jr., A. A. Gould, J. T. Gulick, W. D. Hartman, A. Hyatt, J. C. Jay, Y. Kondo, I. Lea, J. W. Mighels, M. C. Neal, W. Newcomb, W. H. Pease, L. Pfeiffer, H. A. Pilsbry, L. A. Reeve, E. A. Smith, E. R. Sykes, and D'A. A. Welch in the Museum of Comparative Zoology are listed. If the holotype or lectotype is not found there, its location is included if known. New lectotype selections are made only for the figured types of Newcomb, Pfeiffer, and Reeve in The Natural History Museum, London, and those of Newcomb now in the Paleontological Research Institute, Ithaca, New York.

INTRODUCTION

"Evidence exists for a *minimum* of 1,461 recognizable endemic taxonomic units of Hawaiian land snails, comprising 931 species, 332 subspecies, and 198 unjudged varieties." Thus spake the late Alan Solem (1990: 27). Immanuel Kant claimed that he was awakened from his dogmatic slumber on reading the work of David Hume, which led to his work *The Critique of Pure Reason,* and, in a much smaller way, Solem's dogmatic assertion led to the present study, even though this list of types could not contribute to refuting his assertion as to the number of taxonomic units of Hawaiian land snails.

However, since the present work was begun, Cowie, Evenhuis, and Christensen (1995), in a *Catalog of the Native Land and Freshwater Mollusca of the Hawaiian Islands,* suggest that there are "763 nomenclaturally valid species" of endemic land snails. In another paper by Cowie, Nishidra, Basset, and Gon (1995), the authors give a slightly higher number simply because they include 16 questionable ones mentioned in brackets in the *Catalog.*

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Cowie (1995) further calls attention to the difficulty of arriving at an exact taxonomic number for the land species but correctly states that the *Catalog* is the most rigorous, verifiable compilation we yet have, and with this your author is in complete agreement. Even including the few freshwater forms, we still have a total well under 800 named species. Solem's figure of 1,461 taxonomic units seems to have been taken off the chandelier, like imaginary bids at an auction gallery.

The present work does not claim to be more than the title suggests. No estimate of the valid species is attempted, but even a cursory examination of the named material appears to indicate that a modern study of all the Hawaiian land and freshwater mollusks would result in fewer valid species and subspecies being recognized than anyone has yet suggested.

Although previous monographers such as Cooke, Kondo, Pilsbry, Solem, and Welch have attempted to indicate relationships among species, Cowie and colleagues and your present author follow in the footsteps of the great sixteenth century encyclopedist, Conrad Gesner, who alphabetically listed the Latin names of the animals. This had a considerable effect on the arrangement of the text when the work was translated into German, as was pointed out by Ley (1968: 129). Let us hope that the named taxa of Hawaiian nonmarine gastropods are not assigned English names by government decree!

The collection of Hawaiian land and freshwater mollusks in the Museum of Comparative Zoology is probably only exceeded by that in the Bernice Pauahi Bishop Museum. The MCZ, founded in 1859, is fortunate to include the collection of the Boston Society of Natural History, begun in 1830. It is not surprising that Mighels, Gould, and C. B. Adams were sent specimens by, among others, the Reverend Edward Johnson, who lived at Waioli, near Hanalei (Johnson, 1949: 217), for, since 1820, the American Board of Commissioners for Foreign Missions (Congregational)[2] in Boston had been busily sending clergy to the then Sandwich Islands. Among them was Peter Johnson Gulick, who was dispatched in 1827. He was the father of John Thomas Gulick, who was born in Kauai, and grew up to be a student of the Achatinellidae and an evolutionist. By 1850 the Board decided that the Christianization of the Hawaiian Islands was sufficiently complete to begin the return of the missionaries, but it offered full title to the houses in which they were living if they wished to stay in the islands. Among the families that remained were those of Baldwin, Cooke, and Gulick.

Many of the descendants of those who set out to do good did very well. Austin (1921: 91), whose father was Associate Justice of the Supreme Court under Kamehameha V, and executor of William Harper Pease's will, mentioned his friend Charles Reed Bishop from New York State, founder of the banking firm Bishop and Co., who married the Princess Pauahi. She was the great-granddaughter of Kalahiopuu I, the King of Hawaii at the time of Captain Cook's visit (1778), and of Kamehameha I, his successor, who completed the conquest of the other islands. When Mrs. Bishop died, she placed more than 434,300 acres of her royal lands in a perpetual trust and created the Kamehameha School as its sole beneficiary; the Bishop Museum, despite its name, receives nothing from this trust. The school's campus covers some 600 acres and overlooks Honolulu Harbor. It now enrolls 3,000 students from kindergarten through high school.[3] Her husband founded the Bernice

[2] Their vast archives, one of the most fruitful mines for those doing research on the Hawaiian Islands, are now deposited in Houghton Library at Harvard University (see Dodge, 1965: 183).

[3] "Bishop [Trust] put barely one-third of its $244 million in fiscal 1993 earnings into education. Of the rest, about $100 million became new fodder for an intricate web of commercial enterprises and investments—a sum unheard of among other major charities, which spend most of their earnings on core op-

Pauahi Bishop Museum in her honor during 1889 at Kalihi, a western suburb of Honolulu.

On the Fourth of July in 1894, a Republic was declared with Sanford B. Dole as President; a second appeal for annexation was made to President McKinley in 1898, and the islands were formally organized into the Territory of Hawaii. This same year, the preface to Volume 1, Number 1, of the *Occasional Papers of the Bishop Museum* listed Dole as the president of the board of Trustees and William T. Brigham as director. This is the museum where Cooke, Neal, and Kondo, discussed later, spent their professional lives, the early history of which is so interestingly told by Rose (1980).

The other important collection of Hawaiian land and freshwater mollusks is in the Academy of Natural Sciences of Philadelphia. It may not be as extensive as the aforementioned collections, but it is rich in type specimens, especially those of Baldwin, Cooke, and Pilsbry, which were studied by Baker (1963).

THE COLLECTORS (O. P. Emerson, E. J. Meadows, D. Thaanum)

In addition to the sketches of the authors whose types are in the Museum of Comparative Zoology, accounts are provided of Oliver Pomeroy Emerson, Edmund J. Meadows, and Ditlev Thaanum, portions of whose collections are now in the MCZ.

O. P. Emerson (1845–1938) was the son of one of the fifth band of missionaries to arrive in Honolulu. After graduating from Williams College in 1868 and from Andover Theological Seminary in 1871, he also became a missionary. Emerson made a collection of about 950 lots of Achatinellidae, mainly from Oahu, which he bequeathed to the MCZ. He also wrote an account called *Pioneer Days in Hawaii* (1928), in which he mentioned collecting *pupu kani oi-oi* (the shrill-voiced shell), as the *Achatinella* were locally called, and his relations with the neighboring Gulicks.

Little is known about Edmund J. Meadows, but in a letter that came with his collection to the MCZ he stated that he was in Honolulu in 1920 and while hiking in 1925 he saw his first achatinellids. He did not begin collecting them seriously until 1930 after receiving instructions from C. Montague Cooke, Jr. From 1932 until 1942, he was associated with William H. Meinecke, whose collection is in the Bishop Museum. Others with whom Meadows collected were Brickman Lyman, Leopold Blackman, Irwin Spalding, and George Arnemann. The MCZ purchased the Meadows collection in 1947 for $325. It was evaluated by Kondo (1954), who was impressed that it contained representatives of 40 of the 42 species of *Achatinella* that he recognized, lacking only *A. solitaria* Newcomb and *A. thaanumi* Pilsbry and Cooke. It consisted of 653 lots totaling 9,225 specimens and was accompanied by 39 hand-drawn maps, which show every locality at which collections were made. Upon examining the collection in the MCZ, Welch (1958: 125) disagreed with Kondo; he thought it badly mixed and suggested the following:

> The only way the MCZ Meadows collection, as it stands today, could be made reliable would be to send it to Honolulu and have each lot carefully compared with the Meinecke collection to determine which lots were collected with Meinecke. However, there still would always be a question about many localities and some lots would be difficult to determine.

Ditlev Thaanum (1867–1963) was born in the province of Jutland, Denmark. At the age of 9 or 10 he was sent to the family of a printer and publisher, and at the end of 1886 he ended his apprenticeship. After traveling in the United States, he ended

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erations. For the year ended June 30, 1993, Bishop's five governing trustees earned $820,000 each, payments calculated, in unusual fashion, partly as a percentage of the trust's tax free investment income." (Alix M. Freedman and Laurie P. Cohen, *The Wall Street Journal*, April 25, 1995, p. 1. See also *The Wall Street Journal*, May 5, 1995, p. B4; and James Dooley, *The Honolulu Advertiser*, May 16, 1993.)

up in Honolulu in 1894 and never completed the world voyage he had projected. He developed an interest in shells and became one of the great collectors along with his brother-in-law Daniel Kuhns, who later changed his name to Langford. Much of the material that Cooke and Pilsbry published on the land-snail families Achatinellidae and Amastridae was collected by Thaanum or by Thaanum and Kuhns (subsequently as Thaanum and Langford). His own splendid collection of over 4,000 lots of Hawaiian land and freshwater shells, rich in paratypes, was presented to this museum (MCZ) in 1953. Though Thaanum spent his life in the printing trade, he wrote almost nothing himself, but some 30-odd species were named after him based on specimens he collected (Rehder, 1969: 44).

THE COLLECTORS AND TAXONOMISTS

Charles Baker Adams, 1814–53

The most recent account of the life of C. B. Adams is that by Clench and Turner (1950). This paper was written after his collection, which had been at Amherst College, Amherst, Massachusetts, for nearly 90 years, was transferred to the Museum of Comparative Zoology in 1942.

Adams entered Yale University in 1830, but in his sophomore year he transferred to Amherst College, from which he graduated with honors. After spending a few years as Professor of Chemistry and Natural History at Middlebury College, Middlebury, Vermont, he returned permanently to Amherst College in 1847 as Professor of Zoology and Astronomy. He died of yellow fever while visiting his friend and fellow conchologist Robert Swift at St. Thomas in the Virgin Islands.

Adams' main interests were the Western Atlantic and Eastern Pacific marine mollusks, as well as the land shells of Jamaica. Though he never traveled to Hawaii, he described eight taxa (seven new) of *Achatinella* from the Hawaiian Islands; these were collected by Henry Dimond, who resided at Honolulu on Oahu. When a taxon was represented by a single specimen, that specimen was regarded as the holotype by Johnson and Boss (1972), whereas for the remaining taxa lectotypes were selected. All of the species were figured by Johnson and Boss.

César-Marie Félix Ancey, 1860–1906

The life of C.-M. F. Ancey was briefly sketched by Fischer (1908), followed with a complete bibliography of his works on mollusks. Géret (1909) made a list of all the taxa introduced by Ancey, including the original references and type localities, and, having acquired the collection, offered it for sale.

The land and freshwater types from the Hawaiian Islands were purchased by the Bernice Pauahi Bishop Museum in 1908. Brigham (1909) mentions in his Director's Report of 1908 that "Dr. Cooke . . . has been engaged in cataloguing the important collection of the late M. Ancey, now belonging to this Museum." Of the 125 Hawaiian species and subspecies described by Ancey, type material of 31 are to be found in the Museum of Comparative Zoology, received through earlier exchanges or later from the Bishop Museum.

David Dwight Baldwin, 1831–1912

D. D. Baldwin was born in Honolulu and spent his childhood at Waimea, Hawaii, and his boyhood at Lahaina, Maui. From 1844 to 1851, he attended Punahou School, where he was prepared for college by the Reverend Daniel Dole. He graduated from Yale College in 1857, with honors, receiving the prize for astronomy. Returning to the Islands, he became principal of the Lahaina School, and except for seven years when he was manager of the Kohala Plantation (where he introduced the so-called Lahaina sugar cane, to which the plantation owed its success), his professional life was spent in education. Baldwin became Inspector-General of Schools, and

during his administration the number of schools where English was the basis of instruction increased from 5 to 100.

Pilsbry (1912: 82) pointed out that, between the period of Gulick and Newcomb, Baldwin was alone in publishing original work on the Achatinellidae. While the major part of his collection appears to be in the B. P. Bishop Museum, the Museum of Comparative Zoology has an extensive collection that either he or his son, E. D. Baldwin, originally presented to Oberlin College, Ohio.

Because there is no complete published list of the 54 species he described, they are all included here, with references to the primary types, most of which are in the Academy of Natural Sciences of Philadelphia (Baker, 1963), though some are in the B. P. Bishop Museum. Syntypes, paratypes, or paralectotypes of 23 of these are in the Museum of Comparative Zoology. The bibliography herein of Baldwin is believed to be complete.

Theodore Dru Alison Cockerell, 1866–1948

Cockerell, a zoologist interested mainly in entomology and malacology, was born at Norwood, England. After being Curator of the Public Museum in Kingston, Jamaica, for a few years, he spent most of his career as Professor of Zoology at the University of Colorado from 1906 to 1934.

Cockerell published over 3,000 articles on zoology, 147 of them in *The Nautilus* between 1887 and 1947. He described one land snail, *Enodonta* (*Thaumatodon*) *cookei*, from the Hawaiian Islands. An interesting biography and complete bibliography of Cockerell's multiferous publications was written by Weber (1965).

Charles Montague Cooke, Jr., 1874–1948

Cooke's grandfather, Amos Starr Cooke, went to Hawaii in 1836 with the eighth company of missionaries sent by the American Board of Commissioners of Foreign Missions. He was co-founder of the firm of Castle and Cooke and founder of the Royal School for the children of the Hawaiian chiefs. His son, C. M. Cooke, Sr., started the Bank of Hawaii and was a director of the more important business firms, an intimate of Charles Reed, and a trustee of the Bernice P. Bishop Trust and the Bishop Museum. After the overthrow of the Hawaiian Monarchy, Cooke went to Washington to assist in preparing the treaty of annexation. It was into this powerful family that Cooke, Jr., was born.

Young Cooke attended Punahou School and Oahu College. In the family tradition, he also attended Yale University, receiving his Ph.D. in 1901. At Yale, Cooke studied under the eminent zoologist Addison E. Verrill, who took him on a field trip to Bermuda, where Cooke met his future wife, Eliza Lefferts (Johnson, 1989). In 1902, he became an assistant in the Bishop Museum, where he was to spend his professional life primarily in the study of the land shells of the Indo-Pacific. Kondo and Clench (1952) wrote a detailed account of Cooke's life and listed all of his described species. Of the species he described from the Hawaiian Islands with Pilsbry in the various volumes of the *Manual of Conchology*, with Kondo or by himself, 107 are represented here.

Augustus Addison Gould, 1805–1866

The life of A. A. Gould, a Boston physician and author of numerous works on mollusks, including the description of those brought back by the United States Exploring Expedition (1838–42), was written by Johnson (1964). The Gould collection was sold by his heirs to the New York State Museum in Albany, New York, in 1867 for $6,000. The supposed types of 362 species were segregated from the main collection as "The Gould Type Collection" and in 1959 were placed on permanent loan at the Museum of Comparative Zoology. A few years later, the remainder of the collection was deposited in the United States National Museum, with

permission to divide it with the MCZ, as seemed desirable.

Gould was born on a farm in New Ipswich, New Hampshire. At the age of 15, though by then in charge of the farm, he was able to study at the New Ipswich Appleton Academy. In 1821, at the age of 17, he entered Harvard College, where, by frugality and application, he graduated with respectable grades. It was here that he developed an interest in natural history. During 1829–30, he was a student at the Massachusetts General Hospital under Drs. James Jackson and Walter Channing and was in attendance at the first use of ether as an anesthetic in an operation. Dr. Gould became active in the Boston Society of Natural History, which held its first meeting at Dr. Channing's house in 1830, and was an active member until his death from Asiatic cholera in 1866.

Johnson (1964) recataloged all of the mollusks described by Gould and found the figured specimens or selected lectotypes for most of the 34 land and freshwater mollusks he described from the Hawaiian Islands. All of these are included here, even if no type material was found in the Museum of Comparative Zoology. In his *Otia Conchologia* (1862), Gould sometimes changed the generic placement for some of the species; such revisions are indicated by brackets in the list herein.

John Thomas Gulick, 1832–1923

Gulick, the son of a Presbyterian missionary, as was D. D. Baldwin, was among the earliest of the native-born students of Hawaiian land snails. Both Baldwin and Gulick attended Punahou School under the direction of the Reverend Daniel Dole, Gulick from the day the school opened on July 11, 1842. While still a boy, Gulick made an extensive collection of the Achatinellidae, most of it under an altitude of 1,500 feet. He brought this collection to the United States when he attended Williams College, from which he graduated in 1859.

Gulick attended Union Theological Seminary between 1861 and 1863. He spent his active missionary life in China and Japan until his retirement in 1899. As a temporary residence, Gulick and his wife settled in Oberlin, Ohio, where they could leave their children to obtain their education at the college, before retiring to Oahu, the island he loved so much.

Before beginning his missionary work, Gulick was encouraged by the members of the Lyceum of Natural History of New York to begin the publication in its Annals of 73 new species of Achatinellidae, illustrated with hand-colored plates. Having already thought that geographical isolation had something to do with the variation he observed between some of the forms he had described, the publication of Darwin's *On the Origin of Species* the year he graduated from college made him a life-long evolutionist. Gulick (1888) recognized two important components of evolution and used the terms *monotypic evolution*, or "transformation in time," and *polytypic evolution*, or "transformation in space." Though Gulick and later Romanes (1897) understood these two very different components of evolution, this insight "was largely forgotten again after 1897, until Mayr (1942) and others revived it during the evolutionary synthesis" (Mayr, 1982: 401), though Gulick (1905) continued to promulgate his ideas. Gulick was also the first person to suggest that much evolutionary change is simply a result of chance variation, a thesis not entirely settled to this day (Mayr, 1982: 555; see also Carson, 1987).

Reif (1985) showed how Gulick developed a broad theory that corrected deficiencies in Darwin's theory. Gulick anticipated central concepts of population genetics. He emphasized nonadaptive differences between populations, but he did not "deny the existence of adaptive variation in snails" (Mayr, 1980: 133). One reason for Gulick's work being almost forgotten was the ascendancy of the neo-Lamarckians at the time of his writing and his use of many neologisms, which are rendered

pellucid by Reif in a glossary. Amundson (1994) quotes Gulick's earliest evolutionary insight, "[A]ll those *Achatinellae* never came from Noah's Ark." This was a very bold statement, given his religious background, but not surprisingly he rejected the fatalism of Herbert Spencer's Social Darwinism and, by 1905, was a confirmed socialist. Amundson (1994: 139) quotes the "Dialectical Biologist" Richard C. Lewontin as seeing Gulick's "False Biology and Fatalism" (1908) as primarily a commentary on the third of Karl Marx's "Theses on Feuerbach."

In 1872, Gulick made up 20 sets out of his collection. The third of these was sold to the Boston Society of Natural History, which later, through the efforts of Alpheus Hyatt, also obtained (for $600 in gold) the first set, which included the figured specimens of all the species he had described. The fate of the remaining sets was set forth by Clench (1959) but is not relevant here. The Society's mollusk collection was transferred to the Museum of Comparative Zoology after 1914, when the former became the New England Museum of Natural History (now Museum of Science). Also included were 18 folios of Gulick's notes. The collection he presented to Oberlin College was also transferred to the Museum of Comparative Zoology in 1959.

An extensive and interesting account of Gulick's life and scientific work, including a complete bibliography, was published by his son, Addison (Gulick, 1932), who also presented unpublished manuscripts to the MCZ Mollusk Department library (reprint nos. 8553, 11375, and 12097).

All of Gulick's systematic papers are listed here but, of the theoretical papers, only those cited are included.

William Dell Hartman, 1817–99

Hartman was born in East Pikeland Township, Chester County, Pennsylvania, in 1817, the descendant of natives of Schwerin, Hesse Kassel, Germany. After local schooling, Hartman attended what was then the famous school of Jonathan Gause and the academy of Jonathan Strode. He graduated from the Medical Department of the University of Pennsylvania at the age of 21. After graduation, he settled in West Chester, where his practice became very extensive.

Hartman devoted all of his spare time to the study of natural history. He did extensive research on the genus *Partula* based mainly on specimens from Andrew Garrett and also on the genus *Achatinella* (1888). One of these, *Achatinella nattii* 'Baldwin' Hartman, is represented in the MCZ. Pilsbry (1899: 62) included a bibliography of Hartman's work and mentioned that his extensive collection of Achatinellidae was sold to the "Bremen Museum" (presumably the Übersee-Museum) sometime before his death.

Alpheus Hyatt, 1838–1902

Alpheus Hyatt spent his childhood in Baltimore, Maryland, on his family's estate, known as Wansbeck, then outside the city. By the time of Hyatt's death (at 64 while on his way to a meeting of the Boston Society of Natural History), it had become a hospital and lay well within the city limits. Hyatt was sent at an early age to the Maryland Military Academy and later spent one year at Yale before becoming a student of Louis Agassiz at Harvard College. After graduating in 1862, Hyatt served in the Union Army throughout the Civil War, retiring with the rank of Captain. It was not until nearly 30 years later that his relatives, having found themselves on opposite sides of the conflict, became reconciled.

In 1867, Hyatt, along with E. S. Morse, A. S. Packard, F. W. Putnam, and A. E. Verrill, became associated with the newly formed Peabody Institute in Salem, Massachusetts, financed by George Peabody. These fellow students of L. Agassiz soon founded *The American Naturalist*. In 1870, Hyatt was appointed custodian (the title was changed to curator in 1881) of the Boston Society of Natural History, where he remained until his death 32 years later.

Hyatt stated that he became an evolu-

tionist in 1859 upon reading Darwin's *On the Origin of Species*, the same year he began his studies under L. Agassiz, who would resist evolutionary thought throughout his life. Hyatt was not a Darwinian but became, along with the vertebrate paleontologist Edward Drinker Cope, a leading exponent of the neo-Lamarckian (American, not French) school. They believed that important new characters arose from the activities of animals themselves. Hyatt posited that the sequence of embryonic stages paralleled the sequence of ancestral adults and that phylogeny could be read from ontogeny. He used this principle of recapitulation to reconstruct the evolutionary history of ammonoids. As this was not natural selection, he answered the question of what determines the sequence of new stages in phylogeny with his theory of "racial senescence." This theory was best developed in his paper on *Planorbis* (1880), which argued that species, like individuals, have a determined cycle of youth, maturity, and old age leading to extinction. This idea had credence, especially among paleontologists, until the modern evolutionary synthesis was accomplished in the 1940s.

A biographical memoir of Hyatt was written by Brooks (1909), which was accompanied by a bibliography. His evolutionary ideas were discussed by Gould (1972). Hyatt became interested in the evolutionary history of the Achatinellidae and, as mentioned previously, he had the first and third sets of Gulick's material and could say, "There are at present under this roof about fourteen or fifteen thousand shells of this one group . . . there are also about six thousand more, the property of Mr. Oleson, of Worcester" (Hyatt, 1898: 283). When Gulick, while in Boston in 1899, visited the Boston Society of Natural History he found that

> [a]s an aid to the investigation Hyatt had constructed a large relief model of Oahu, with colored pins and threads that visualized the geographical relationships of the species. All his life Gulick had cherished the dream of seeing his collection itself laid out in geographical order on a great map, and this model supplied the nearest approach that he ever saw to the dream come true. (A. Gulick, 1932: 321)

Because Hyatt died before his manuscript was complete, it was finished by H. A. Pilsbry and, thus, co-authored as Hyatt and Pilsbry (1911). Although Pilsbry did not share many of Hyatt's views, he included Hyatt's articles on classification of Amastrae (1911: 358) and on the genealogy and distribution of the Achatinellidae in his volumes.

Types of 19 of the species described by Hyatt (or Hyatt and Pilsbry) were located in the collection of the Boston Society of Natural History that was deposited in the Museum of Comparative Zoology after 1914, when the Society became the New England Museum of Natural History.

John Clarkson Jay, 1808–91

Jay was a physician, active in the Lyceum of Natural History of New York, where he served as librarian (1834–35) and as treasurer (1844–46). He made a collection of shells that at the time of his death was probably the largest in the United States. Its growth was documented in his *Catalogue of Recent Shells in the Cabinet of John C. Jay, MD*, which first appeared in 1835, with ever-expanding editions in 1836, 1839, and 1850 and a supplement in 1852. The second and third editions contain descriptions of new species, but only one, *Achatina bicolor*, described in the third edition, is of concern here. The Jay collection and library were eventually presented by Catherine L. Wolfe to the American Museum of Natural History, which later disposed of Jay's own interleaved, annotated *Catalogue* (1850), which was purchased by your author and is now in the Department of Mollusks, Museum of Comparative Zoology. The molluscan types in the AMNH were listed by Richards and Old (1969).

Yoshio Kondo, 1910–90

Yoshio Kondo was born on Maui. C. Montague Cooke, Jr., took an interest in

him when he observed the young Japanese-Hawaiian serving as engineer on the sampan *Myojin Maru,* which the Bishop Museum had hired to conduct its Mangarevan Expedition in 1934. Cooke appointed Kondo Assistant in Malacology and encouraged him to earn his Bachelor's and Master's degrees at the University of Hawaii. He received his Ph.D. from Harvard University in 1955. His thesis, *A Revision of the Family Partulidae,* is still mostly unpublished. Cowie (1993) published a bibliography of Kondo and listed his taxa. Six of Kondo's Hawaiian taxa are represented here from two of his papers (1952, 1960). In both, he respectfully attributed senior authorship to Cooke.

Isaac Lea, 1792–1886

Isaac Lea was born into a prosperous family of wholesale merchants who were members of the "Society of Friends," or Quakers. In 1821, he married Frances Anne Carey, whose father, Matthew Carey, owned one of the largest publishing houses in the United States at that time. "Although the firm had already been promised to Henry, the son now offered to relinquish part of his 'birthright' and take Isaac into the firm as junior partner" (Kaser, 1957: 21). The new firm, H. C. Carey & I. Lea, began on January 1, 1822. Lea retired from Carey and Lea in 1851, probably not much missed by his brother-in-law. Though he remained active in the firm until his retirement, Lea's real interest was in geology and land and freshwater mollusks.

By 1852, the year in which he received an honorary doctor of laws degree from Harvard University, he had completed only five volumes of his *Observations on the Genus Unio,* which were reprints of articles he had originally published in the *Transactions of the American Philosophical Society* beginning in 1828. They were eventually completed in 13 volumes after first being published in the *Journal of the Academy of Natural Sciences of Philadelphia.*

In spite of his having been president of the Academy and active in its affairs for many years, Lea left his collections of shells and minerals to the United States National Museum, now the National Museum of Natural History. His life and works were carefully studied by Scudder (1885). Of the several species he described from the Hawaiian Islands, only paratypes of *Melania newcombii* from Oahu are in the Museum of Comparative Zoology.

Jesse Wedgwood Mighels, 1795–1861

Mighels was born in Parsonsfield, Maine, and was teaching school by the time he was 18. He studied medicine under the direction of a local physician, and after attending some medical lectures at Dartmouth College, he was awarded the degree of M.D. in 1823. After marrying Evalina A. Rust of Norway, Maine, the couple lived in Minot, Maine, for nine years, after which they moved to Portland, where Mighels earned a reputation in surgery.

In 1827 he began to collect shells and quickly moved from appreciating their intrinsic beauty to the scientific study of them. When the Portland Society of Natural History was formed, Mighels was elected corresponding secretary at the first election of officers in December 1843. He held that post until he moved to Cincinnati, Ohio, in 1847 to become a professor at the Cincinnati College of Medicine and Surgery. Sometime before 1857, he fell down an open shaft or stairway, sustaining injuries from which he never fully recovered. He returned to Maine, where he died later that same year.

The Mighels collection of shells, consisting of over 3,000 species, was purchased by the Portland Society of Natural History in 1846 for $1,000 but was destroyed by a fire on January 8, 1854. Of the 27 Hawaiian land and freshwater species described by Mighels, listed here, Johnson (1949) was able to locate types of

13 of them from other sources, from which lectotypes were chosen and figured.

Marie Catharine Neal, 1889–1965

Marie C. Neal was brought up in Connecticut. She received her B.A. from Smith College in Northampton, Massachusetts, where she was especially interested in botany. After graduating in 1912, she obtained a job as a stenographer with the Travelers Insurance Company. Later she worked for the Children's Aid Society and in the Geology Department of Yale University for Dr. Herbert E. Gregory until 1920, when he was appointed director of the Bernice Pauahi Bishop Museum in Honolulu. Gregory agreed to find her a position in botany and send for her. The only position open was in the Department of Mollusks, which she accepted.

In Hawaii, she worked for Dr. C. Montague Cooke, Jr., as Assistant Malacologist from 1920 to 1930 while earning a master's degree from Yale with her thesis on Hawaiian marine algae. "Miss Neal's capacity for work was astounding. In 1923 she catalogued 200,000 terrestrial mollusks" (Hartt and Peterson, 1984). As junior author to H. A. Pilsbry and C. M. Cooke, Jr. (1928), she wrote on the land snails of Hawaii. At last, in 1930 she was appointed Botanist and put in charge of the Museum's herbarium. "Thus began what were to be many full and richly productive years." (Doyle, 1965). She wrote one more malacological paper by herself, on Hawaiian Helicinidae (1934). Paratypes of two of the subspecies described there as new, *Pleuroploma laciniosa globuloides* and *P. l. spaldingi,* are in the Museum of Comparative Zoology.

Wesley Newcomb, 1808–92

Newcomb was born in Pittstown, Rensselaer County, New York. Following family tradition, Newcomb studied medicine. After attending the White Plains Academy and Rensselaer Institute, he received his M.D. from Castelton Medical College in Vermont, where he was valedictorian of his class. It was while he was at Rensselaer Institute that Professor Amos Eaton directed his attention to shells as a key to paleontology, but Newcomb became so fascinated with shells that paleontology was largely forgotten.

He settled in California during the Gold Rush year of 1849, but owing to his wife's poor health, he moved to Honolulu in 1850 where he remained until 1855. Here he made his extensive collection of *Achatinella.* Returning to the United States, he settled in Albany, New York, making a trip to Europe in 1857 to study the types of *Achatinella* described by Pfeiffer and others, with Augustus A. Gould as a companion for part of the sojourn. After returning to the United States, he published his "Synopsis of the Genus *Achatinella*" the next year. Most of his writings after this were on other groups of mollusks. Ezra Cornell purchased the Newcomb collection for his new university in 1886 for $15,000. It contained some 10,000 species and was exceeded in size in the United States only by that of the Academy of Natural Sciences in Philadelphia and John C. Jay.

Clarke (1958) established that the paper by Newcomb (1854a), quoted and accepted as having priority by Pfeiffer (1854), which later appeared in the *Proceedings of the Zoological Society of London* (1854b), was published before June of that year and qualifies as a first edition, and that it was the issue available to Pfeiffer. In addition to the copy of this edition studied by Clarke at Cornell is a copy in the library of the Department of Mollusks at the Museum of Comparative Zoology. With the exception of *Achatinella grisea,* which was omitted, all of the mollusks described by Newcomb were listed by Clarke (1958), who also related the life of Newcomb and his role in the study of mollusks.

All of the Hawaiian land mollusks described by Newcomb are included here, as are the catalog numbers of the types in his collection now at the Paleontological Re-

search Institution, Ithaca, New York. The Museum of Comparative Zoology has the set of types that Newcomb sent to his friend Augustus A. Gould. The package had remained unopened in the Gould collection until, with the permission of the United States National Museum, with which the collection had been shared, your author opened it sometime after 1960. It contained nine species not located by Clarke (1960): *Achatinella adamsii, baldwinii, emersonii, greisea, mastersi, melanosis, obesa, pfeifferi,* and *porcellana.*

Clarke was unaware that Welch (1938, 1942, 1954, 1958) had either found the figured types or selected some lectotypes from the original set of types sent to Hugh Cuming that were figured in the *Proceedings of the Zoological Society of London* and were then in the British Museum (Natural History), now The Natural History Museum. They are *Achatinella cestus, elegans, glabra, multilineata, turgida,* and *ovata.*

Seven species not represented elsewhere, described and figured in the *Proceedings of the Zoological Society of London,* are *Achatinella aplustre, hybrida, nivosa, recta, semicarinata, solitaria,* and *venulata,* as well as the "figured holotypes" of most of the nominal species listed here as syntypes. The figured types of these and others have been identified by D'Alte Welch or your author and are selected here as lectotypes.

William Harper Pease, 1824–71

Pease was born in Brooklyn, New York. He joined the Lyceum of Natural History of New York in 1841; traveled with General Winfield Scott to Mexico in 1848; arrived in Honolulu in 1849; and in 1850 applied for citizenship in the Hawaiian Kingdom, purchased land, and became local agent of the Government on Kauai. Returning to Honolulu about 1856, Pease became Commissioner of Water Rights and Rights of Way as well as Assessor of the City of Honolulu.

His main interest was natural history, especially the shells of the Pacific. In a letter of 1865, quoted by Kay (1965: 6), he wrote, "That is all I think or care about." Clench (1975) listed all of the mollusks described by Pease but did not mention the location of any of the type material, which is located in The Natural History Museum, London; Muséum National d'Histoire Naturelle, Paris; Academy of Natural Sciences of Philadelphia, and the Pease collection itself, which was purchased, after his death in 1871, by Louis Agassiz for the Museum of Comparative Zoology.

Johnson (1994) located type material for 45 of the 55 land and freshwater mollusks, included here, that Pease described from the Hawaiian Islands.

Ludwig Pfeiffer, 1804–77

Karl Georg Ludwig Pfeiffer was born in Kassel, Hesse Nassau, Germany, in 1804. He graduated from the *gymnasium* at the age of 16, studied medicine at the University of Göttingen, and at the age of 20 graduated with his M.D. from the University of Marburg. In 1833, Pfeiffer married Louise Philippine Nathusius, and it would appear that her financial endowment was sufficient to allow him to give up medicine to study botany and malacology. In an exercise of brevity, Wheeler (1949: 50) informs us that "his first marital relations were not congenial, and after the death of his three children, he secured a divorce." In 1842 he married Wilhelmina Frederika Wagner of Wetzlar, this time happily; they had five sons and one daughter.

Pfeiffer wrote extensively on land snails and made frequent trips to Paris and London to study specimens and literature not available to him in Kassel. After his death, Pfeiffer's collection and library were sold to Heinrich Dohrn, who removed them to the Museum in Stettin (now Muzeum Naradowe, Szczecin, Poland), which was destroyed during World War II. The present museum there has no material dating from before 1945 (W. Filipowiak, personal communication, 1995). The figured lectotypes of Hawaiian land snails mentioned

here were described from specimens in the collection of Hugh Cuming, now in The Natural History Museum, London.

Henry Augustus Pilsbry, 1862–1957

Pilsbry was born on a farm in Johnson County, Iowa, educated in the public schools of Iowa City, and graduated from the University of Iowa in 1882. He spent his spare time collecting mollusks, and his first paper, written when he was 20, was a list of the land and freshwater shells of Iowa City. He was to publish over 2,000 articles before his death. In 1887, Pilsbry was invited by George Washington Tryon, Jr., then head of the Conchological Section of the Academy of Natural Sciences of Philadelphia, to join the department. Tryon died two months later, leaving the 25-year-old Pilsbry in charge, with the task of completing the volumes on marine gastropods for the *Manual of Conchology*, begun by Tryon, the profits on the sale of which supplied his salary at that time.

"Throughout his life, Henry Pilsbry's most outstanding scientific contributions were in his researches on land snails, and he was known internationally as the preeminent authority on Pulmonata" (Baker, 1958: 79). Most of the 70-odd Hawaiian species introduced by Pilsbry alone or in collaboration with Cooke or Hyatt appeared in the second series of the *Manual of Conchology* between 1910 and 1926, and the figured types were located by Baker (1963). Pilsbry's concept of the species as far as Achatinellidae are concerned is discussed later, under Welch. Clench and Turner (1962) listed most of the species described by Pilsbry.

Lovell Augustus Reeve, 1814–65

Reeve was born at Ludgate Hill, London. His father was a draper and mercer whose brother-in-law, Alderman Waithman, became Lord Mayor of London and later representative of the City of London during four successive Parliaments. Young Reeve distinguished himself in school, winning prizes in Latin and Greek; nevertheless, he was removed from school at the age of 13 and apprenticed to a grocer. A chance encounter with a sailor "with a pocket handkerchief full of shells" (Melvill, 1900: 345) led to his life-long devotion to conchology. He formed an acquaintance with John Edward Gray of the British Museum and later with the prolific collector Hugh Cuming, who had the largest private collection of the time.

In 1843, Reeve began his most ambitious work, the *Conchologia Iconica*, which consisted of a series of illustrated monographs on various molluscan genera, written by himself, drawn on lithographic slates by G. B. Sowerby, Sr., colored by hand, and issued with letterpress. By the time he died, Reeve had described as new some 2,000 species, mostly from the Cuming collection, now in The Natural History Museum, London. All of the 15 *Achatinella* species were from the Cuming collection. Cuming sent examples of four of these to C. B. Adams, whose collection is now in the MCZ. The figured types of these in The Natural History Museum, London, have been identified by D'Alte Welch or your author and are selected here as lectotypes.

Edgar Albert Smith, 1847–1916

E. A. Smith, son of a Keeper of Entomology at the British Museum, was educated privately and at the North London Collegiate School. When barely 20 years old, he became an assistant in the Zoological Department at the same museum as his father. This was a few years before the retirement of John Edward Gray, the then Keeper of Zoology, who put Smith to work on the great shell collection of Hugh Cuming, which the museum had acquired in 1846. The arrangement of the Mollusk Collection was his responsibility when the natural history collections were moved from Bloomsbury to the new British Museum (Natural History) in 1881. Melvill (1917: 151) called attention to Smith's

pamphlet (1906), which detailed the growth of the Mollusk Collection from its beginning and listed the authors whose types are to be found there. Smith described over 2,300 species of mollusks, and it is of interest here that he also served, from 1891 to 1912, on the British Association Committee, which was appointed in 1890 to "[r]eport on the present state of our knowledge of the Zoology of the Sandwich Islands." After his official retirement in 1913, Smith continued to work at the museum until his death at the age of 69 in 1916.

In a paper on Hawaiian Achatinellinae he co-authored with Gulick (1873), Smith described 32 species as new. Seventeen of the figured holotypes and paralectotypes of four others are now in the Museum of Comparative Zoology. The figured specimens of the 11 not included here are presumed to be in The Natural History Museum, London. Trew (1993) listed all of the names introduced by Smith and included a complete bibliography.

Ernest Ruthven Sykes, 1867–1954

Although E. R. Sykes wrote over 100 articles on conchology, almost no information about him has been published in any of the malacological journals. Of his personal life, we have few details, though Swann (1992: 5), whose firm bought Sykes' extensive library in 1948, mentioned that "Sykes's family had a bank which was one of those amalgamated to form Barclay's" and that he had lived in a beautiful old manor house in Dorset.

Sykes devoted particular attention to the nonmarine mollusks of the Indo-Malayan region and of the Indo-Pacific islands. Rees (1954: 23) mentioned that, when his collection was presented to the then British Museum (Natural History) after his death, there was "a fine series representing his work on land Mollusca of Hawaii in *Fauna Hawaiiensis* (1900)." Only three of the Hawaiian species Sykes described are present in the Museum of Comparative Zoology.

D'Alte Aldrich Welch, 1907–70

Welch was born in New York City. He received his Ph.D. from Johns Hopkins University in 1937. Commencing in 1942, he was a professor of biology at John Carroll University in Cleveland, Ohio. In 1970, he was shot to death in a hold-up outside the Racquet Club in Cleveland (Abbott and Baker, 1970). He was survived by his wife, Ann Frances (Goddard), and five children.

Welch was primarily a student of the Hawaiian Achatinellidae, studying them with the same ardor with which his mentor, Henry Edward Crampton, had studied the *Partula* of the Society Islands. From Crampton, Welch received many ideas regarding the biometrical treatment of distribution problems. Welch also applied the then-emerging modern species concept to his understanding of the fauna.

In the first (1938: 14) of his four major studies (1938, 1942,[4] 1954, 1958), Welch discussed the taxonomic concepts of Pilsbry, who recognized three grades of speciation (Pilsbry, May 1914: xxv). Welch agreed with Pilsbry, who considered races under Grade I to be species because there are no integrating or hybrid forms between two races, A and B, in the same valley. Regarding Grade II, Pilsbry considered geographic races (i.e., with a definite and consistent distribution) that blend with other races through hybrid or undifferentiated colonies where the geographic races meet to also be species. Welch correctly pointed out that two *Achatinella* that integrate are not distinct species; they are subspecies of a single species. Pilsbry's Grade III does not have taxonomic status. The term subspecies and its concept (Mayr and Ashlock, 1991: 430) were not available to Pilsbry or Welch. Describing

[4] Printed during the World War II paper shortage, this study made national news. The original Smithsonian issue was probably set for 250 copies, but by mistake 25,000 were actually printed of this 256-page monograph on the variation of a single species of *Achatinella*.

borderline cases involving populations that have acquired some but not all of the attributes of species rank, they cover Welch in particular in his use of the term "variety," which he used in the sense of population dynamics and not, as Mayr and Ashlock (1991: 432) mention, to describe "an ambiguous term of classical (Linnaean) taxonomy for a heterogeneous group of phenomena including variations of the phenotype, phena, domestic breeds, and geographic races."

Welch made copious use of the MCZ *Achatinella,* especially in his later papers (1954, 1958). The collection contains figured paratypes of some of his subspecies, as well as figured specimens that do not have taxonomic status.

Welch was also a distinguished collector and bibliographer of antiquarian children's books. His final work on the subject was published posthumously (1972).

REMARKS

The following catalog includes all of the types of Hawaiian land and freshwater mollusks represented in the Museum of Comparative Zoology. If a taxon is not represented there by a holotype or lectotype, every effort has been made to locate it elsewhere if one exists. All of the Hawaiian land and freshwater taxa, even if no type material could be found, are included of those described by C. B. Adams, D. D. Baldwin, A. A. Gould, J. T. Gulick, J. W. Mighels, W. Newcomb, and W. H. Pease. It is arranged alphabetically by species or subspecies. In addition to the original reference, subsequent citations are also included if they provide the first figure of a type specimen or other relevant material. Type localities have been modified to the extent that the island is always given first. Data in brackets, with the exception of generic changes made by Gould in his *Otia Conchologia* (1862), have been found on original labels, are additions or corrections from recent maps, or are comments by this author.

James (1996: 100) somewhat reluctantly excuses Cowie, Evenhuis, and Christensen (1995) for not using the glottal stop and macron in correctly writing locality data in the Hawaiian language. James's reference to Pukui and Elbert (1971), actually revised and enlarged in 1986, is to a Hawaiian–English, English–Hawaiian dictionary, which is by no stretch of the imagination a gazetteer. The *Atlas of Hawaii,* edited by Armstrong and Bier (1983), does list many localities in Hawaiian. No apology is offered here for not changing the original orthography of any of the localities; this should not be interpreted as an English-only policy.

In decades past, if revisers such as Cooke, Pilsbry, Welch, and the present author were able to locate the single figured or measured syntype, it was usually regarded as the holotype. For example, the single figured specimens of Gulick's taxa have always been regarded as holotypes. Most of the designations included in this paper were made long before the promulgation of the third edition of the *International Code of Zoological Nomenclature* (1985), which invalidated this practice under Article 74(b): ". . . should another syntype or syntypes be discovered [the first subsequent author is to be regarded] to have chosen a lectotype." If this change is to be made it is left here, in these instances, to a subsequent reviser.

Baker (1963, 1964) listed all of the types of land snails in the Academy of Natural Sciences of Philadelphia and used his own system of abbreviations for type designation, which have been interpreted here as follows:

TOD type by original designation [holotype]

TOM type because only one example was included in the original description or was indicated by only one set of dimensions . . . [holotype]

TSD type by subsequent selection, followed by "now" if apparently first designated in these lists . . . [lectotype]

In a few instances, Welch refigured Newcomb's types, regarding them as holotypes or lectotypes. He further identified the figured type from among the others in most of the lots, at The Natural History Museum, London, and at Cornell University. Having been privileged to examine all of these types, as well as some figured by Pfeiffer, Reeve, Smith, and Sykes, in the former institution, these are selected as lectotypes in compliance with *ICZN* 74(b).

The paper by Cowie, Evenhuis, and Christensen (1995) was a very valuable tool in helping your author correct numerous errors and deficiencies from appearing in the following list of references. Unfortunately, Cowie et al. were not aware that the authorship, and occasionally the type localities, of many of the new species described in the monographs by Hyatt and Pilsbry or Pilsbry and Cooke published in the *Manual of Conchology* appeared only on the plate captions, hence there are discrepancies in some of the references given here.

ACKNOWLEDGMENTS

It gives me great pleasure to thank those people whose cooperation eased the task of gathering information. Dr. Fred Naggs, of the Mollusca Section, The National History Museum, London, in addition to answering many questions, kindly made it possible for me to borrow all of the Newcomb types, as well as many others that I had requested. Dr. Robin Hadlock Seeley, Professor of Zoology, Cornell University, Associate Curator in Malacology, Paleontological Research Institution, Ithaca, New York, also kindly lent all of the Newcomb material requested and supplied a valuable list of the Newcomb material that Welch had had on loan for 20 years. Dr. Robert H. Cowie, Associate Malacologist, Bernice Pahuai Bishop Museum, made it possible to include data concerning many of the primary types in that institution. Ms. Karen J. Kroslowitz also assisted in this effort. Ms. Janet A. Short, Catalog Librarian, supplied all of the biographical data on Marie Catharine Neal, which this author would never have been able to locate. Dr. Paula M. Mikkelsen, Delaware Museum of Natural History, ascertained that there was no Mighels material in that institution.

Mrs. Marion D. Britz began putting the manuscript on a computer many years ago and was very patient with the author's many changes and corrections, as has been Ms. Kate Tuttle, who in addition to her patience and good humor has produced the final effort. Ms. Tanya Kausch cheerfully helped in many ways, especially by curating much of the material.

The "anonymous" reviewers who kindly identified themselves, Drs. Alan R. Kabat and Robert H. Cowie, are deserving of special thanks for meticulously correcting the manuscript.

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ABBREVIATIONS

In general, this author disdains references that merely give a date, forcing the use of the bibliography over and over. To partially alleviate this problem, the principal references are cited in the catalog by the following abbreviations.

AJC	*American Journal of Conchology*
ALNHNY	*Annals of the Lyceum of Natural History of New York*
AMNH	American Museum of Natural History, New York, New York
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania
BJNH	*Boston Journal of Natural History*

BMCZ	*Bulletin of the Museum of Comparative Zoology*
BMNH	British Museum, Natural History, London; now The Natural History Museum
BPBM	Bernice Pauahi Bishop Museum, Honolulu, Hawaii
BSMF	*Bulletin de la Société Malacologique de France*
BSNH	Boston Society of Natural History, Boston, Massachusetts; now The Museum of Science
CU	Cornell University; W. A. Newcomb collection now at the Paleontological Research Institution, Ithaca, New York
JdeC	*Journal de Conchyliologie*
JofM	*Journal of Malacology*
MofC	*Manual of Conchology*
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MNHN	Muséum National d'Histoire Naturelle, Paris
OPM	*Occasional Papers on Mollusks*
PANSP	*Proceedings of the Academy of Natural Sciences of Philadelphia*
PBSNH	*Proceedings of the Boston Society of Natural History*
PCANS	*Proceedings of* the California Academy of Natural Sciences
PMSL	*Proceedings of the Malacological Society of London*
PZS	*Proceedings of the Zoological Society of London*
USEE	United States Exploring Expedition
USNM	United States National Museum, Washington, D.C.; now The National Museum of Natural History, Smithsonian Institution

Titles of other journals cited in the catalog are usually given in full.

TYPES OF LAND AND FRESHWATER MOLLUSKS FROM THE HAWAIIAN ISLANDS IN THE MUSEUM OF COMPARATIVE ZOOLOGY INCLUDING ALL OF THE HAWAIIAN LAND AND FRESHWATER TAXA INTRODUCED BY C. B. ADAMS, D. D. BALDWIN, A. A. GOULD, J. T. GULICK, J. W. MIGHELS, W. NEWCOMB, AND W. H. PEASE

abavus Hyatt and Pilsbry, *Amastra* (*Amastrella*)
1911, MofC (2) **21**: 255, pl. 42, figs. 4, 5 (Molokai: Pukoa; fossil). Figured syntypes BPBM 23483; syntype MCZ 97644.

abberans Hyatt [in] Hyatt and Pilsbry, *Amastra* (*Amastra*) *bigener*
1911, MofC (2) **21**: 300, pl. 44, fig. 8 (Maui). Holotype USNM 117264; paratypes MCZ 136883 ex Gulick collection 1549.

abbreviata Ancey, *Tornatellina*
1904a [1903], JdeC **51**: 298, pl. 12, figs. 7, 8 (Maui: Kaupakalua). Not mentioned by Fischer-Piette (1950: 171); syntype ANSP 111850 figured by Pilsbry and Cooke (1916, MofC (2) **23**: 268, pl. 55, figs. 12, 13); syntypes BPBM 18421; syntypes MCZ 165800 and 199568.

abbreviata Reeve, *Achatinella*
1850, *Conchologia Iconica 6, Achatinella*, pl. 3, species 19 ([Oahu: Palolo, *teste* Pilsbry and Cooke (1913: 123)]; Cuming collection). Lectotype, here selected, BMNH 1992195/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992195/2; MCZ 298275 ex Cuming.

accineta Mighels, *Achatina*
1845, PBSNH **2**: 20 (Oahu). The type figured by Reeve (1849, *Conchologia Iconica 5, Achatina*, pl. 19, species 101) not located in BMNH by Naggs (personal communication); not located by Johnson (1949: 220).

acicula Pilsbry and Cooke, *Tornatellides perkinsi*
1915, MofC (2) **23**: 225, pl. 49, figs. 3, 4 (Oahu: Punaluu). Figured syntypes BPBM 36256; syntypes ANSP 111839 and MCZ 97581.

acuminata Cooke, *Amastra* (*Metamastra*) *subrostrata*
1933, BPBM *Occ. Pap.* **10**(6): 21, pl. 2, fig. 10 (Oahu: Waianae Mountains, Luahalei, southeast side of valley, high up the sides in a damp glen). Figured holotype and paratypes [listed as cotypes] BPBM 10773; paratypes MCZ 97624.

acuminata Gould, *Achatinella* [*Leptachatina*]

1847, PBSNH **2**: 200 (Kauai); 1852, USEE **12**: 87, pl. 7, fig. 100; 1862, *Otia Conch.*, pp. 34, 244. "Single broken specimen in Smithsonian [USNM 5502]. A careful search through Gould's collection in Albany did not produce another specimen" (Cooke, 1911: 5).

acuta, Newcomb, *Achatinella*
1854, PZS **21**: 142 (preprint p. 16), pl. 23, fig. 36 (Oahu: Lehui; single specimen). Non *A. acuta* Swainson 1828 is *A. elongata* Newcomb 1854, *teste* Newcomb (1858: 328). Newcomb (1858: 328) asserts that figure 36 is not *acuta* but is based on the same specimen of *A. soror* as figure 38. Specimens identified by Newcomb [idiotypes] CU 29898 from Maui; not located in BMNH by Naggs (personal communication).

adamsi Newcomb, *Achatinella*
1853, ALNHNY **6**: 19 (Maui: Makawao); 1854, PZS **21**: 137 (preprint p. 11), pl. 22, fig. 20 (East Maui). Syntypes MCZ 294932; not located in BMNH by Naggs (personal communication); not found in CU by Clarke (1960: 145); syntypes BMNH 1995100 and CU [not numbered] ex MCZ 294932.

admodesta Mighels, *Pupa*
1845, PBSNH **2**: 19 (Oahu). Lectotype MCZ 177005 selected by Johnson (1949, OPM *1*: 221, pl. 27, fig. 17).

adusta Gould, *Achatina* [*Carelia*]
1845, PBSNH **2**: 26 (Sandwich [Hawaiian] Islands); 1862, *Otia Conch.*, p. 194. Not located by Johnson (1964: 38).

aemulator Pilsbry [in] Hyatt and Pilsbry, *Amastra* (*Metamastra*)
1911, MofC (2) **21**: 190, pl. 38, fig. 7 (Oahu: Kahauiki; Thaanum). Holotype BPBM 23486; paratypes MCZ 31165 ex Thaanum.

affinis Newcomb, *Achatinella*
1854, PZS **21**: 142 (preprint p. 16), pl. 23, fig. 35 (East Maui: Kula). Lectotype, here selected, BMNH 1992252/1 is the figured type; paralectotypes BMNH 1992252/2; MCZ 142823 and 294934; supposed paralectotypes CU 29901, though from Haleakala.

agglutinans Newcomb, *Achatinella obesa*
1854, PZS **21**: 143 (preprint p. 17), pl. 23, fig. 39a (no locality [Wailuku, *teste* Hyatt and Pilsbry (1911: 283)]). Syntypes CU 30037 from East Maui; not located in BMNH by Naggs (personal communication); not in MCZ.

albalabia Welch, *Achatinella bulimoides*
1954, PANSP **106**: 73, pl. 1, fig. 7 (Oahu: [North Poamoho Stream, North Branch]). Holotype BPBM 10511; paratypes BPBM 50410; paratypes MCZ 138644 from lower part of Pa Kanaka Valley [and additional type lots from other localities].

albescens Gulick, *Achatinella*
1858, ALNHNY **6**: 237, pl. 8, fig. 57 (Oahu: Waimea, Pupukea, Waialei, Kahuku, Hauula [and] Kaawa [Kaaawa]). Holotype only, MCZ 39866 from Waialei, "the metropolis of the species."

albolabris Newcomb, *Achatinella*
1854, PZS **21**: 149 (preprint p. 23), pl. 24, fig. 56 (Oahu: Waianoe [Waianae]). Lectotype, here selected, BMNH 1992261/1 is the figured type; paralectotypes BMNH 1992261/2; CU 29902; MCZ 294944.

albospira Smith [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 77, pl. 10, fig. 8 (Oahu: Ewa). Holotype only, MCZ 39903.

alexandri Cooke [in] Pilsbry and Cooke, *Gulickia*
1915, MofC (2) **23**: 112, pl. 28, fig. 7 (West Maui: Maunahooma [Maunahoomaha], Honokowai). Holotype BPBM 14148 according to Cowie, Evenhuis, and Christensen (1995: 78), from "valley E. of Maunahooma above Japanese camp, 800–1,000 feet," but the label reads "Hahakea, West Maui"; paratype MCZ 97549 correctly labeled "Maunahooma," suggests that the label represents a copying error.

alexandri Newcomb, *Achatinella*
1865, PCANS **3**: 182 (West Maui: elevation of 7,500 feet); 1866, AJC **2**: 216, pl. 13, fig. 14. Lectotype, here selected, CU 29903A, though slightly smaller than the figure; paralectotypes CU 29903; not in MCZ; not found in ANSP by Baker (1963).

alpha Pilsbry and Cooke, *Helicina laciniosa*
1908, BPBM *Occ. Pap.* **3** (2): 203, fig. 5 (Oahu: Mt. Tantalus). Holotype BPBM 14904; paratypes MCZ 191073.

ambigua Pease, *Limnaea*
1870, AJC **6**: pl. 3, fig. 5 (Hawaiian Islands). Holotype ANSP 21240a, *teste* Baker (1964: 152); paratypes MCZ 73469.

ambusta Pease, *Auriculella*
1868, JdeC **16**: 345 ([Oahu: Waianae Mountains]). Lectotype MCZ 45152, selected by Johnson (1994, BMCZ **154**: 6, pl. 2, fig. 10); paralectotypes MCZ 298488.

ampla Newcomb, *Achatinella*
1854, PZS **21**: 137 (preprint p. 11), pl. 22, fig. 19 (Oahu: Kolau [Koolau]). Lectotype, here selected, BMNH 1992210 is the figured and only type, *teste* Welch; paralectotypes CU 29904; not in MCZ.

ampulla Gulick, *Achatinella*
1856, ALNHNY **6**: 200, pl. 7, fig. 29 (Maui: Honukawai). Holotype only, MCZ 39872 from Lahaina [sic].

analoga Gulick, *Achatinella*
1856, ALNHNY **6**: 227, pl. 7, fig. 47 (Oahu: Halawa). Holotype only, *teste* Gulick, MCZ 39845.

anceyana Baldwin, *Achatinella* (*Partulina*)
1895, PANSP **47**: 223, pl. 10, fig. 16 (Maui: Makawao). Figured holotype ANSP 65707a, *teste* Baker (1963: 193).

anceyana Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 39, pl. 1, figs. 18, 19 (Hawaii: Mana; fossil). Holotype BPBM 12037; paratypes MCZ 97674.

anceyana Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 253, pl. 26, figs. 3–6 (Hawaii:

Olaa). Holotype BPBM 11050; paratypes MCZ 180242.

anceyana Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa (Infranesopupa)*
1920, MofC (2) **25**: 293, pl. 28, figs. 2, 3 (Hawaii: Humuula). Holotype BPBM 11072; paratypes MCZ 78795.

anceyanum Pilsbry and Cooke, *Elasmias*
1915, MofC (2) **23**: 118, pl. 31, figs. 7, 8 (West Maui: Maunahooma [Maunahoomaha]). Holotype BPBM 14147; paratype MCZ 97552.

angulata Pease, *Carelia adusta*
1871, JdeC **18**: 403 ([Kauai]). Lectotype ANSP 23434 selected by Baker (1963: 197) figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 116, pl. 20, fig. 16); paralectotypes MCZ 45167.

angusta Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa (Limbatipua) newcombi*
1920, MofC (2) **25**: 315, 309, fig. 4 (Kauai: Kipu). Holotype BPBM 20227; paratypes MCZ 78807.

annosa Cooke, *Amastra (Amastrella) rugulosa*
1917, BPBM *Occ. Pap.* **3** (3): 230, pl. A, fig. 9 (Kauai: Hanamaulu plains south of Wailua River; Pleistocene). Holotype and paratypes [listed as cotypes] BPBM 41998; paratypes MCZ 97592.

anthonii Newcomb, *Achatinella*
1861, PCANS **2**: 93 (Kauai); 1866, AJC **2**: 210, pl. 13, fig. 2. Lectotype, here selected, CU 29905A is the figured type, so marked; paralectotypes CU 29905; MCZ 141330; not found in ANSP by Baker (1963).

antiqua Baldwin, *Amastra (Amastra)*
1895, PANSP **47**: 233, pl. 11, fig. 47 (Oahu: Ewa). Figured holotype ANSP 65716a, *teste* Baker (1963: 197).

antiqua Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 250, pl. 21, figs. 8, 9, 11 (Oahu: Manoa in Pleistocene deposits along the Upper Manoa Road). Holotype BPBM 11047 (fig. 11); paratypes MCZ 78760.

antiqua Pease, *Leptachatina*
1870, JdeC **18**: 94 (Kauai); Crosse, 1876, JdeC **24**: 97, pl. 3, fig. 6. Holotype in MNHN, *teste* Fischer-Piette (1950: 149).

apicata 'Newcomb' Pfeiffer, *Achatinella*
1856, PZS **23**: 210 ([Oahu]). Lectotype BMNH 1992194/1 selected by Welch (1942, *Smithsonian Miscellaneous Collections* **103**(1): 152, pl. 11, fig. 2); paralectotype BMNH 1992194/2; paralectotypes CU 30135.

aplustre Newcomb, *Achatinella*
1854, PZS **21**: 147 (preprint p. 21), pl. 23, fig. 51 (Oahu: Kolau [Koolau]). Is *A. johnsoni* Newcomb, *teste* Newcomb (1858: 330). Lectotype, here selected, BMNH 1992222 is the figured and only type, *teste* Welch; not found in CU by Clarke (1960: 146); not in MCZ.

arborea Sykes, *Leptachatina*
1900, *Fauna Hawaiiensis* **2**(4): 357, pl. 11, fig. 21 (Hawaii: Kona at 4,000 feet, Perkins; Olaa, Hilo, Baldwin). Lectotype, here selected, BMNH 1900.12.18.550 is the figured type, so labelled; paralectotypes BMNH 1900.12.18.551–555; BPBM 14918, *teste* Cooke (1918: 292); MCZ 202598 from Olaa ex Thaanum and 174022 from Hilo ex Putzeys collection.

arenarum Pilsbry and Cooke, *Amastra (Cyclamastra) umbilicata*
1914, MofC (2) **23**: 23, pl. 2, figs. 1–4 (Molokai: sand dunes of Moomomi; Pleistocene). Syntypes BPBM 74000; ANSP [no number] and MCZ 97607.

armatus Mighels, *Bulimus*
1845, PBSNH **2**: 19 (Hawaii). Lectotype MCZ 177001 selected by Johnson (1949, OPM **1**: 221, pl. 27, fig. 15); paralectotypes MCZ 156034.

arnemani Welch, *Achatinella bulimoides*
1958, PANSP **110**: 174, pl. 13, figs. 4–6 (Oahu: Punaluu–Kahana Ridge). Holotype ANSP 192583 (fig. 4); paratype MCZ 170044 (fig. 6), from Kahana.

aspera Baldwin, *Laminella*
1908, *Nautilus* **22**: 68 (West Maui: Wailuku Valley). Holotype ANSP 104693a figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 197, pl. 53, fig. 10), *teste* Baker (1963: 197); paratypes MCZ 97669.

assimilis Newcomb, *Achatinella*
1854, PZS **21**: 148 (preprint p. 22), pl. 23, fig. 53 (West Mani [Maui]). Lectotype, here selected, BMNH 1992259/1 is the figured type, so marked; paralectotypes BMNH 1992259/2; CU 29907; MCZ 142903.

attenuata Cooke, *Leptachatina (Leptachatina)*
1911, MofC (2) **21**: 69, pl. 7, figs. 45, 46 (Kauai: Haleiele, Makaweli, Waiakoali, Ekuala, Hanalei). Holotype BPBM 12012; paratypes MCZ 97682 from Haleiele.

attenuatus Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 219, pl. 48, figs. 3, 4 (Oahu: Manoa; fossil). Holotype BPBM 14134; paratypes MCZ 97512.

augusta Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 74, pl. 9, fig. 7 (Oahu: Waialae, also in Waulupe and Palolo). Lectotype, here selected, BMNH 1992199/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992199/2; MCZ 159662 from Waialae, 159657 and 159658 *both* from Waulupe, and 159660 from Palolo.

aurantium Pilsbry and Cooke, *Laminella gravida*
1915, MofC (2) **23**: 54, pl. 1, figs. 3–5 (Oahu: above Waiahole; Thaanum [and other localities]). Lectotype ANSP 109904a (fig. 4) selected by Baker (1963: 197); paralectotypes MCZ 31202 and 190962 *both* ex Thaanum.

aurora Pilsbry and Cooke, *Amastra (Cyclamastra) obesa*
1914, MofC (2) **23**: 18, pl. 4, figs. 9–12 (East Maui: Auwahi, at about 4,200 feet elevation; Thaanum). Lectotype ANSP 109830a (fig. 9) selected by Baker

(1963: 197); paralectotypes MCZ 97614 ex Cooke and 125312 ex Thaanum.

aurostoma Baldwin, *Amastra*
1896, *Nautilus* **10**: 31 (Lanai). Syntypes ANSP [no number] figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 240, pl. 26, figs. 13, 14); [holotype] ANSP 68874a [which type not indicated], *teste* Baker (1963: 198); [paratypes] MCZ 135769.

auwahiensis Pilsbry and Cooke, *Amastra* (*Heteramastra*) *subsoror*
1914, MofC (2) **23**: 48, pl. 5, figs. 8–10 (East Maui: Auwahi, at 4,200 ft.; Thaanum). Lectotype ANSP 109836a (fig. 8) selected by Baker (1963: 197); paralectotypes MCZ 97614 ex Cooke; 31184 and 125310 *both* ex Thaanum.

avus Pilsbry and Cooke, *Leptachatina oryza*
1915, MofC (2) **23**: 5, pl. 10, figs. 12–16 (Molokai: sand dunes of Moomomi; Pleistocene). Lectotype ANSP 108982a (fig. 12) selected by Baker (1963: 197); paralectotype MCZ 97684.

bacca Pease, *Vertigo*
1871, PZS for 1871: 462 (Hawaii: Kalapana [Puna District]). Specimens lost, *teste* Pease.

badia Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 230, pl. 11, fig. 40 (Oahu: Ewa). Figured type in Baldwin collection, not found in BPBM, but 4 syntypes BPBM 55535, *teste* Kroslowitz (personal communication); not found in ANSP by Baker (1963).

baileyana Gulick, *Achatinella*
1856, ALNHNY **6**: 202, pl. 7, figs. 31a, b (Maui: Wailuku Mountain). Holotype MCZ 39862 (fig. 31a); paratype MCZ 39860 (fig. 31b is variety b); paratypes MCZ 136543–136545.

baldwini Ancey, *Helicina*
1904, PMSL **6**: 126, pl. 7, fig. 24 (Kauai: Kipu). Syntypes MCZ 191041.

baldwini Ancey, *Nesopupa*
1904, PMSL **6**: 122, pl. 7, fig. 13 (Molokai; Maui: Kaupakalua). Holotype BPBM 18698 from Kaupakalua, *teste* Cooke and Pilsbry (1920: 287); paratypes MCZ 78790 and 199563.

baldwiniana Cooke [in] Pilsbry and Cooke, *Lyropupa rhabdota*
1920, MofC (2) **25**: 241, pl. 20, figs. 7, 8 (West Maui: Iao). Holotype BPBM 11042; paratypes MCZ 78753.

baldwiniana Pilsbry [in] Hyatt and Pilsbry, *Amastra* (*Amastra*)
1911, MofC (2): **21**: 292, pl. 43, figs. 4, 5 (West Maui: Wailuku). Lectotype ANSP 104719a (fig. 4) selected by Baker (1963: 197); paralectotype MCZ 97647.

baldwinii Newcomb, *Achatinella*
1854, PZS **21**: 155 (preprint p. 29), pl. 24, fig. 72 (Ranai [Lanai]). Is *A. magna* C. B. Adams, *teste* Newcomb (1858: 319). Syntypes MCZ 141484, 141485, and 294958. Not located in BMNH by Naggs (personal communication), or in CU [not numbered] by Clarke (1960: 146); syntypes BMNH 1995101 and CU ex MCZ 294958.

balteata Pease, *Leptachatina*
1870, JdeC **18**: 91 (Kauai: [Waimea]); Crosse, 1876, JdeC **24**: 97, pl. 4, fig. 4. Holotype in MNHN, *teste* Fischer-Piette (1950: 149); paratypes MCZ 142986.

balteata Pilsbry and Cooke, *Partulina* (*Perdicella*) *helena*
1912, MofC (2) **22**: 17, pl. 4, fig. 7 ([Molokai: Kahanui]). Holotype ANSP 109053a, *teste* Baker (1963: 193); paratypes MCZ 190508.

berniceia Pilsbry and Cooke, *Helicina*
1908, BPBM *Occ. Pap.* **3** (2): 207, fig. 11 (Kauai: Limahuli; fossil). Holotype BPBM 14909; paratypes MCZ 191038.

beta Pilsbry and Cooke, *Helicina laciniosa*
1908, BPBM *Occ. Pap.* **3** (2): 202, fig. 4 (Oahu: Kapalama). Holotype BPBM 14903; paratypes MCZ 191099.

bicolor Jay, *Achatina*
1839, *Catalogue of Shells*, 3d ed., p. 119, pl. 6, fig. 3 ([Kauai]). Figured holotype AMNH 56094 from Jay 5203, *teste* Richards and Old (1969: 15); paratype MCZ 181208 ex AMNH.

bicolor 'Gulick' Pfeiffer, *Achatinella*
1859, *Monographia Heliceorum Viventium* **4**: 529 (Oahu: Lehui). Syntypes MCZ 39899 ex Gulick collection 94 and 159680 ex Gulick collection 1433; the "holotype" figured by Welch (1938: 97, pl. 9, fig. 1) BMNH [no number]; not located in BMNH by Naggs (personal communication).

bigener Hyatt [in] Hyatt and Pilsbry, *Amastra* (*Amastra*) *affinis*
1911, MofC (2) **21**: 300, pl. 44, figs. 7, 8 (Maui: [Kula]). Lectotype ANSP 57685a (fig. 7) selected by Baker (1963: 197); paralectotypes MCZ 136884 and 136888; *both* ex Gulick collection 588.

biplicata Newcomb, *Achatinella*
1854, PZS **21**: 156 (preprint p. 30), pl. 24, fig. 75 (Ranai [Lanai]). Lectotype, here selected, BMNH 1992246/1 is the figured type; paralectotypes BMNH 1992246/2; CU 29912; MCZ 141486 and 294953.

boettgeri Cooke and Pilsbry [in] Pilsbry, *Pronesopupa* (*Pronesopupa*)
1920, MofC (2) **26**: 8, pl. 1, fig. 17 (Oahu: Tantalus). Holotype BPBM 11030; paratypes MCZ 78815.

borcherdingi Hyatt and Pilsbry, *Amastra* (*Amastra*)
1911, MofC (2) **21**: 266, pl. 41, figs. 1–4; pl. 40, figs. 2–6 (Molokai). Lectotype ANSP 57714a (fig. 1) selected by Baker (1963: 197); paralectotypes MCZ 154727 ex BSNH 13446.

breviata Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 231, pl. 11, figs. 45, 46 (Oahu: Palolo, Halawa). Figured holotype ANSP 65723a (fig. 45), *teste* Baker (1963: 197); paratypes MCZ 135765.

brevicula Pease, *Helicter* (*Leptachatina*)
1869, JdeC **17**: 169 (Kauai). Measured holotype

and paratype in MNHN, *teste* Fischer-Piette (1950: 72); paratype ANSP 57802 figured by Cooke (1910, MofC (2) **21**: 24, pl. 8, fig. 54); paratype MCZ 45195.

brevis Cooke, *Leptachatina* (*Leptachatina*) *pachystoma*
1910, MofC (2) **21**: 52, pl. 8, fig. 53 (Kauai: Haleieie). Holotype BPBM 12007; paratypes MCZ 202463 ex Thaanum.

brunnea Smith [in] Gulick and Smith, *Auriculella*
1873, PZS for 1873: 88, pl. 10, fig. 23 (Molokai; Lanai). Holotype only, MCZ 39915 from Molokai.

brunneus Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 238, pl. 51, figs. 5, 6 (Oahu: Nuuanu near the Pali). Holotype BPBM 36266; paratype MCZ 97511.

buddii Newcomb, *Achatinella*
1854, PZS **21**: 155 (preprint p. 29), pl. 24, fig. 73 (Oahu: Palolo). Lectotype, here selected, BMNH 1992231/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992231/2; CU 29912; MCZ 294933 and 315851.

bulbosa Gulick, *Achatinella*
1858, ALNHNY **6**: 253, pl. 8, fig. 71 (East Maui: Honuaula [and] Kula). Holotype MCZ 39886; paratypes MCZ 136637 and 159729; *all* from Kula.

cacuminis Pilsbry and Cooke, *Auriculella diaphana*
1915, MofC (2) **23**: 77, pl. 24, figs. 11, 12 (Oahu: head of Kalihi-Moana-lua ridge, Mauna Kope). Figured holotype ANSP 108277a, *teste* Baker (1963: 193); paratypes MCZ 31187 and 73046.

caduca Mighels, *Succinea*
1845, PBSNH **2**: 21 (Oahu). Lectotype MCZ 39645 selected by Johnson (1949, OPM **1**: 221, pl. 27, fig. 16).

caesia Gulick, *Achatinella*
1858, ALNHNY **6**: 234, pl. 8, fig. 53 (Oahu: Waimea). Holotype only, MCZ 39869.

caesiapicta Welch, *Achatinella bulimoides*
1954, PANSP **106**: 95, pl. 2, figs. 14–19 (Oahu: Kawailoa). Holotype ANSP 92486 (fig. 16); paratypes ANSP 92486 (figs. 17, 17a, b); [paratype] MCZ 170192 (fig. 14).

canaliculata Baldwin, *Achatinella* (*Newcombia*)
1895, PANSP **47**: 226, pl. 10, figs. 28, 29 (Molokai: Halawa). Figured syntypes ANSP 65713; [holotype] ANSP 65713a [which type not indicated], *teste* Baker (1963: 193); [paratypes] ANSP 65713 and MCZ 190529.

candida Pilsbry and Cooke, *Partulina* (*Baldwinia*) *horneri*
1913, MofC (2) **22**: 108, pl. 17, figs. 3, 4 (Hawaii: above Kukuihalele [name and type locality on plate caption]); 1914, *Ibid.*, p. 365, pl. 54, fig. 12. Lectotype ANSP 108203a (pl. 17, fig. 3) selected by Baker (1963: 193); paralectotypes MCZ 190885.

canella Gould, *Succinea*
1846, PBSNH **2**: 184 (Maui); 1852, USEE **12**: 27, pl. 2, figs. 20, 20a, b; 1862, *Otia Conch.*, p. 29. Holotype USNM 5420; paratypes MCZ 169072 and 161661.

caperata Gould, *Vitrina*
1846, PBSNH **2**: 181 (Kauai); 1852, USEE **12**: 10, pl. 1, figs. 9, 9a; 1862, *Otia Conch.*, p. 26. Holotype USNM 5409; paratypes MCZ 135612.

capillata Pease, *Helix*
1866, AJC **2**: 292 (Sandwich [Hawaiian] Islands); 1871, PZS for 1871: 474 as *Pityx* (Maui). Lectotype ANSP 1975a [now 1975] selected by Solem (1976: 368 [not figured]), is the measured type, *teste* Baker (1963: 232), figured by Johnson (1994: BMCZ **154**: 8, pl. 2, fig. 1); paralectotypes MCZ 17585.

capitosa Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 29, pl. 11, fig. 12 (Oahu: Waianae Mts., back of Leilehua). Holotype BPBM 12079; paratype MCZ 97689.

carbonaria Ancey, *Lyropupa*
1904, PMSL **6**: 125, pl. 7, fig. 21 (Oahu: Nuuanu [Valley, near Honolulu], Honolulu). Holotype [in] BPBM 18752, *teste* Cooke and Pilsbry (1920: 236); paratypes MCZ 9600 and 141163.

carinata Gulick [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 83 [not figured] (West Maui: Wailuku). Holotype MCZ 39889; paratypes MCZ 136906. Is *Achatinella obesa agglutinans* Newcomb, *teste* Gulick and Smith (1873: 83).

carinella Baldwin, *Newcombia*
1906, *Nautilus* **19**: 136 (East Maui: Nahiku). Syntypes ANSP 109052 figured by Pilsbry and Cooke (1912, MofC (2) **22**: 57, pl. 2, figs. 1–3); [holotype] ANSP 109052a [which type not indicated], *teste* Baker (1963: 193).

carnicolor Baldwin, *Partulina*
1906, *Nautilus* **19**: 112 (East Maui: Nahiku). Syntypes ANSP 110079 figured by Pilsbry and Cooke (1912, MofC (2) **22**: 58, pl. 12, figs. 13, 14); [holotype] ANSP 110079a [which type not indicated], *teste* Baker (1963: 193); [paratypes] MCZ 135725.

casta Ancey, *Succinea*
1899, PMSL **3**: 272, pl. 12, fig. 10 (Hawaii: Olaa). Holotype BPBM 18982; paratypes MCZ 190646.

casta Newcomb, *Achatinella*
1854, PZS **21**: 134 (preprint p. 8), pl. 22, fig. 12 (Oahu: Ewa. Its northern limit is the valley below Mouna [Mauna] Rua, and half a dozen ravines, south, in the district of Ewa). Lectotype, here selected, BMNH 1992215/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992215/2; CU 29920; MCZ 294924.

castanea Reeve, *Achatinella*
1850, *Conchologia Iconica 6, Achatinella*, pl. 3, species 24 (Sandwich [Hawaiian] Islands; Cuming collection). Lectotype, here selected, BMNH 1992196/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992196/2; MCZ 298276 ex Cuming.

cepulla Gould, *Succinea* [*Helisaga*]
1846, PBSNH **2**: 182 (Hawaii); 1852, USEE **12**: 16, pl. 2, figs. 15, 15a, b; 1862, *Otia Conch.*, pp. 27,

244. Syntype USNM 5415, smaller than measured type; syntypes MCZ 39646, 169114, and 216754.

cerealis Gould, *Achatinella* [*Leptachatina*]
1847, PBSNH **2**: 201 (Oahu: Waianai [Waianae]); 1852, USEE **12**: 90, pl. 7, fig. 99a; 1862, *Otia Conch.* pp. 35, 244. Holotype USNM 5501; not in MCZ.

cervina Gulick, *Achatinella*
1858, ALNHNY **6**: 241, pl. 8, fig. 62 (Oahu: Kahana). Holotype only, MCZ 39835.

cestus Newcomb, *Achatinella*
1854, PZS **21**: 132 (preprint p. 7), pl. 22, fig. 8 (Oahu: Palolo). Lectotype BMNH 1992188/1 is the figured type, selected and refigured by Welch (1942, SMC **103**(1): 31, pl. 4, fig. 9); paralectotypes BMNH 1992188/2: CU 29925; MCZ 25497 and 294947.

cicercula Gould, *Helix* [*Corasia*]
1846, PBSNH **2**: 171 (Hawaii); 1852, USEE **12**: 43, pl. 5, figs. 73, 73a–c; 1862, *Otia Conch.*, pp. 20, 243. Holotype USNM 20948; paratypes MCZ 169080.

cincta Ancey, *Tornatellina*
1903 [1904], JdeC **51**: 297, pl. 12, figs. 5, 6 (East Maui: Makawao, Kaupakalua; West Maui: vallée d'Iao; Oahu; Molokai). Lectotype BPBM 18500 from Makawao selected by Cooke [in] Pilsbry and Cooke (1916, MofC (2) **23**: 263, pl. 55, fig. 1); paralectotypes MCZ 165799 from Kaupakalua. Cowie, Evenhuis, and Christensen (1995: 82), finding paralectotypes under the same number as the figured lectotype, instead of merely recataloging them, regard the lectotype selection itself as invalid, which it will be if the figured specimen cannot be identified.

cindrella Hyatt [in] Hyatt and Pilsbry, *Amastra affinis*
1911, MofC (2) **21**: 300, pl. 45, figs. 1, 2 (Maui: Kula). Figured syntypes MCZ 136882 ex Gulick collection 1546.

cingula Mighels, *Achatinella*
1845, PBSNH **2**: 21 (Oahu). Syntypes Jay collection 5207 and Newcomb collection. Not located by Johnson (1949: 224), or subsequently.

citrina 'Mighels' Pfeiffer, *Achatinella*
1848, *Monographia Heliceorum Viventium* **2**: 234 ([Molokai]). Lectotype MCZ 156493 selected by Johnson (1949, OPM **1**: 224, pl. 27, fig. 14); paralectotypes MCZ 156492.

clathratula Ancey, *Lyropupa*
1904, PMSL **6**: 125, pl. 7, fig. 19 (Hawaii: Olaa). Holotype BPBM 18742, *teste* Cooke and Pilsbry (1920: 245); paratypes MCZ 78751.

clausinus Mighels, *Bulimus*
1845, PBSNH **2**: 20 (Hawaii). Not located by Johnson (1949: 224).

cochlea Reeve, *Achatina*
1849, *Conchologia Iconica 5, Achatina*, pl. 1, species 5 (Peru [Kauai]; Cuming collection). The figured type not located in BMNH by Naggs (personal communication); syntypes MCZ 156148 and 156149, *both* ex Cuming.

cognata Gulick, *Achatinella*
1858, ALNHNY **6**: 240, pl. 8, fig. 60 (Oahu: Hakipu, Waikane). Holotype MCZ 39841; paratype MCZ 40159; *both* from Hakipu.

compacta Pease, *Helicter* (*Labiella*)
1869, JdeC **17**: 172 (Maui: [Palauea]). Lectotype MCZ 45196, selected by Johnson (1994, BMCZ **154**: 9, pl. 4, fig. 5); paralectotypes MCZ 298489.

compacta Pease, *Limnaea*
1870, AJC **6**: 6, pl. 3, fig. 4 (Oahu). Syntypes MCZ 302381; not located in ANSP by Baker (1964: 151). Is *Physa mexicana* Philippi [introduced], *teste* D. W. Taylor (Johnson, 1994, BMCZ 154: 8).

compta Pease, *Helicter* (*Partulina*)
1869, JdeC **17**: 175 (Molokai). Holotype in MNHN figured by Fischer-Piette (1950, JdeC **90**: 73, fig. 54); paratypes MCZ 25826 and 25828.

concidens Gulick, *Achatinella*
1858, ALNHNY **6**: 234, pl. 8, fig. 54 (Oahu: Waimea). Holotype only, MCZ 39817.

concinna Newcomb, *Achatinella*
1854, PZS **21**: 157 (preprint p. 31), pl. 24, fig. 79 (Ranai [Lanai]). Lectotype, here selected, BMNH 1992267/1 is the figured type; paralectotypes BMNH 1992267/2; CU 29932; MCZ 294973.

concolor Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 31, pl. 6, figs. 9, 10 (Molokai: Kamalo). Holotype BPBM 12038; paratypes MCZ 202515 and 202516.

concolor Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 75, pl. 9, fig. 1 (Oahu: Ewa). Holotype only, MCZ 39875.

conica Baldwin, *Amastra*
1906, *Nautilus* **19**: 137 (Hawaii: Hamakua). Syntype [no number] Baldwin collection figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 313, pl. 47, fig. 8); [holotype] ANSP 104711a *teste* Baker (1963: 197).

conicospira Smith [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 86, pl. 10, fig. 10 ([Oahu]). Holotype only, *teste* Smith, MCZ 39894.

conifera Smith [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 85, pl. 10, fig. 11 (East Maui: Kula). Holotype MCZ 39896; paratypes MCZ 136857 figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 303, pl. 45, figs. 12, 13).

coniformis Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 80, pl. 9, fig. 23 (Oahu: Kalaikoa and Ahonui, very rare in Wahiawa and Helemano). Holotype MCZ 39911; paratypes MCZ 147161 and 147163; *all* from Ahonui; paratypes MCZ 147162 from Kalaikoa.

consanguinea Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 73, pl. 9, fig. 3 (Oahu: Ahuimanu). Holotype only, MCZ 39878.

contigua Pease, *Melania*
1870, AJC **6**: 7 (Kauai). Lectotype MCZ 74887, selected by Johnson (1994, BMCZ **154**: 9, pl. 4, fig. 19); paralectotypes MCZ 298908; not located in ANSP by Baker (1964: 181).

contracta Gulick, *Achatinella*
1858, ALNHNY **6**: 239, pl. 8, fig. 59 (Oahu: Kaawa [Kaaawa], Hauula). Holotype only, MCZ 39852 from Kaaawa.
cookei Baldwin, *Achatinella* (*Apex*)
1895, PANSP **47**: 220, pl. 10, fig. 15 (Oahu: Waiau, Ewa). Lectotype ANSP 65692 selected by Welch (1942, SMC *103*(1): 76, pl. 7, fig. 8); improperly regarded as invalid by Baker (1963: 194).
cookei Cockerell, *Endodonta* (*Thaumatodon*)
1933, *Nautilus* **47**: 58 (Oahu: on a dead tree-fern on Mt. Tantalus [Koolau Mts.]). Holotype ANSP 158823 studied but not figured by Solem (1976: 213); paratype MCZ 106309.
cookei Pilsbry, *Leptachatina*
1914, *Nautilus* **28**: 61 (Oahu: Kawaihapai, the bluff is the last terrace of the Waianae Mountains). Lectotype ANSP 110593a, first set of dimensions, selected by Baker (1963: 197); paralectotype MCZ 97702 ex Cooke.
cooperi Baldwin, *Partulina*
1906, *Nautilus* **19**: 135 (East Maui: Hana). Syntype figured by Pilsbry and Cooke (1912, MofC (2) **22**: 72, pl. 19, fig. 12); [holotype] ANSP 110087a, *teste* Baker (1963: 194).
cornea Newcomb, *Achatinella*
1854, PZS **21**: 141 (preprint p. 15), pl. 23, fig. 32 ([Oahu: Waialua]). Lectotype, here selected, BMNH 1992249/1 is the figured type; paralectotypes BMNH 1992249/2; CU 29933; MCZ 294929.
corrugata Gulick, *Achatinella*
1858, ALNHNY **6**: 248, pl. 8, fig. 66 (Oahu: Hakipu). Holotype MCZ 39857; paratypes MCZ 147066.
costata Pease, *Vertigo*
1871, PZS for 1871: 461 (Hawaii: [Kona]). Listed as an undetermined species by Pilsbry and Cooke (1920: 272). Holotype MCZ 45238, *teste* Cooke on label; figured by Johnson (1994, BMCZ **154**: 10, pl. 2, fig. 20); not MCZ 45327, which is a *Goniobasis* as mentioned by Pilsbry and Cooke (1926: 224).
costulata Gulick, *Achatinella*
1856, ALNHNY **6**: 177, pl. 6, fig. 5 (Oahu: Pupukea, Waimea, and Kawailoa). Holotype MCZ 39828; paratypes MCZ 45202 and 136991; *all* from Pupukea; paratypes MCZ 136992 from Waimea and MCZ 136990 from Kawailoa.
costulosa Pease, *Leptachatina*
1870, JdeC **18**: 90 (Kauai); Crosse, 1876, JdeC **24**: 97, pl. 3, fig. 4 (Kauai: [Moloaa]). Holotype in MNHN, *teste* Fischer-Piette (1950: 149); paratype MCZ 45191.
costulosa Pease, *Vertigo*
1871, PZS for 1871: 462 (Hawaii). Lectotype ANSP 57806 selected by Johnson (1994, BMCZ **154**: 10, pl. 2, fig. 22); paralectotypes MCZ 32294; not located in BMNH, *teste* Mordon (personal communication).
crassa Newcomb, *Achatinella*
1854, PZS **21**: 155 (preprint p. 29), pl. 24, fig. 71 (Ranai [Lanai]). Lectotype, here selected, BMNH 1992233/1 is the figured type; paralectotypes BMNH 1992233/2; CU 29936; MCZ 294943.
crassilabrum Newcomb, *Achatinella*
1854, PZS **21**: 141 (preprint p. 15), pl. 23, fig. 31 (Oahu: Waianoe [Waianae]). Lectotype, here selected, BMNH 1992248/1 is the figured type; paralectotypes BMNH 1992248/2; CU 29940; MCZ 294939 and 294975.
crassula Smith [in] Gulick and Smith, *Auriculella*
1873, PZS for 1873: 88, pl. 10, fig. 22 (East Maui: Makawao). Holotype only, MCZ 39914.
crocea Gulick, *Achatinella*
1856, ALNHNY **6**: 210, pl. 7, fig. 36 (Maui: Waihee). Holotype only, MCZ 39846.
cryptoportica Gould, *Helix* [*Corasia*]
1846, PBSNH **2**: 171 (hab.?); 1852, USEE **12**: 44, pl. 5, figs. 72, 72a–c (Oahu); 1862, *Otia Conch.*, pp. 20, 243. Lectotype USNM 5474; paralectotypes MCZ 169110.
crystallina Gulick, *Achatinella*
1856, ALNHNY **6**: 186, pl. 6, fig. 14 (Oahu: Mokuleia). Holotype MCZ 29831; paratypes MCZ 45204.
cucumis Gulick, *Achatinella*
1856, ALNHNY **6**: 225, pl. 7, fig. 45 (Oahu: Kalihi). Holotype only, MCZ 39844, is variety b.
cumingi Newcomb, *Achatinella*
1853, ALNHNY **6**: 25 (Maui: Hale-a-ka-la); 1854, PZS **21**: 150 (preprint p. 24), pl. 24, fig. 79. Lectotype, here selected, BMNH 1992224/1 is the figured type, so marked; paralectotypes BMNH 1992224/2; CU 29941; MCZ 25917, 135507, and 294930.
cumingiana Pfeiffer, *Spiraxis*
1855, PZS **23**: 106, pl. 32, fig. 1 (Kanai [Kauai]; Newcomb, Cuming collection). The figured type not located in BMNH by Naggs (personal communication); syntypes BMNH 1996009; possible syntypes MCZ 57120 ex Newcomb.
curta, Newcomb, *Achatinella*
1854, PZS **21**: 144 (preprint p. 18), pl. 23, fig. 43 (Oahu: Waialua). Lectotype, here selected, BMNH 1992217/1 is the figured type, so marked; paralectotypes BMNH 1992217/2; CU 29942; MCZ 294963.
cyclostoma Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 234, pl. 11, fig. 53 (Kauai: Makaweli). Figured holotype ANSP 65724a, *teste* Baker (1963: 197); paratype MCZ 45258.
cylindrata Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa perlonga*
1920, MofC (2) **25**: 261, pl. 23, fig. 8 (Oahu: Makua). Holotype BPBM 11054; paratypes MCZ 78767.
cylindrata Pease, *Helicter* (*Leptachatina*)
1869, JdeC **17**: 168 (Kauai). Lectotype ANSP 57806 selected by Johnson (1994, BMCZ 154: 11), is the syntype figured by Cooke (1910, MofC (2) **21**: 18, pl. 8, figs. 63, 64); paralectotypes in MNHN, *teste* Fischer-Piette (1950: 72).

cylindrella Cooke, *Leptachatina* (*Leptachatina*) *pachystoma*
1910, MofC (2) **21**: 51, pl. 8, fig. 49 (Kauai: Haleieie). Holotype BPBM 12056; paratypes MCZ 97681 ex Cooke and 202464 ex Thaanum.

cylindrica Newcomb, *Achatinella*
1854, PZS **21**: 134 (preprint p. 8), pl. 22, fig. 11 (Oahu: Waianoe [Waianae]). Lectotype, here selected, BMNH 1992239/1 is the figured type; paralectotypes BMNH 1992239/2; CU 29943; MCZ 141438 and 294952.

cyphostyla Ancey, *Tornatellina*
1904, JofM **11**: 70, pl. 5, figs. 22, 23 (Hawaii: Hamakua District, Palihoukapapa, on the Hamakua slope of Mauna Kea, at an elevation of 4000 feet). "Type" BPBM 18425, *teste* Pilsbry and Cooke (1915: 219); paratypes MCZ 97520.

cyrta Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 268, pl. 23, figs. 9, 10 (Hawaii: Mana; fossil). Figured syntypes BPBM 11060 (fig. 9) and ANSP 119441 (fig. 10); syntypes MCZ 78774.

decepta C. B. Adams, *Achatinella*
1851, *Contributions to Conchology* (8): 127 (Sandwich [Hawaiian] Islands). Lectotype MCZ 156040 selected by Johnson and Boss (1972, OPM **3**: 197, pl. 42, fig. 9); paralectotypes MCZ 278340.

decipiens Newcomb, *Achatinella*
1854, PZS **21**: 153 (preprint p. 27), pl. 24, fig. 68 (Oahu: Kahana). Lectotype, here selected, BMNH 1992230/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992230/2; CU 29944; MCZ 294926.

decorata Pilsbry and Cooke, *Newcombia cinnamomea*
1912, MofC (2) **22**: 12, pl. 14, figs. 2–4 (Molokai: Ahaino and Kupeke). Lectotype ANSP 110072a (fig. 3) selected by Baker (1963: 194); paralectotypes MCZ 190546 from Ahaino, 190544 and 190545 *both* from Kupeke.

decorticata Gulick [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 84, pl. 10, fig. 14 (Oahu: metropolis of the species is Kawailoa. It is also found in Helemano, Opaiula, Waimea, Waialei, and Kahuku). Holotype MCZ 39892; paratypes MCZ 40271, 39890, and 136648; *all* from Kawailoa.

decussatula Pease, *Helix*
1866, AJC **2**: 291 (Sandwich [Hawaiian] Islands); 1871, PZS for 1871: 474 as *Pityn* (Molokai). Specimens identified by Pease [idiotypes] MCZ 17273 and 17274 from Waimea or Wahimi, Kauai; not located in ANSP by Baker (1963: 232) or elsewhere by Solem (1976: 377).

delicata Ancey, *Succinea*
1889, BSMF **6**: 243 (East Maui). Syntypes [labeled paratypes] BPBM 19026; syntypes MCZ 214169.

delicata Cooke, *Amastra* (*Cyclamastra*)
1933, BPBM *Occ. Pap.* **10**(6): 7, pl. 1, fig. 2 (Kauai: Nonou Mts., in high valley just west of peak, 700–900 feet elevation). Figured holotype and paratypes [listed as cotypes] BPBM 10770; paratypes MCZ 97594.

delta Gulick, *Achatinella*
1858, ALNHNY **6**: 231, pl. 8, fig. 50 (Oahu: Kalaikoa, Ahonui, Wahiawa and Helemanu [Helemano]). Holotype only, MCZ 39868 from Wahiawa.

delta Pilsbry and Cooke, *Helicina laciniosa*
1908, BPBM *Occ. Pap.* **3**(2): 201, fig. 2 (Kauai: Ekaula, below Puukapele). Holotype BPBM 14901; paratypes MCZ 191098.

dentata Pease, *Tornatellina*
1871, PZS for 1871: 460 (Hawaii). Lectotype MCZ 28918 selected by Johnson (1994, BMCZ **154**: 11, pl. 4, fig. 9); paralectotypes MCZ 175730.

depicta Baldwin, *Laminella* (*Laminella*)
1895, PANSP **47**: 228, pl. 11, figs. 33–35 (Molokai: Kamalo). Lectotype ANSP 65711a (fig. 35) selected by Baker (1963: 197); paralectotypes MCZ 174076.

dextroversa Pilsbry and Cooke, *Achatinella* (*Bulimella*) *sowerbyana*
1914, MofC (2) **22**: 179, pl. 35, figs. 8–13 (Oahu: Pupukea; Thaanum). Lectotype ANSP 108128a (fig. 10) selected by Baker (1963: 194); paralectotypes MCZ 31149 ex Thaanum.

diaphana Smith [in] Gulick and Smith, *Auriculella*
1873, PZS for 1873: 87, pl. 10, fig. 25 (Oahu: the typical forms are from Olomana and Kailua; also found in Palolo, Makiki, and Kalihi). Holotype MCZ 39909; paratypes MCZ 159509; *both* from Olomana.

dimondi C. B. Adams, *Achatinella*
1851, *Contributions to Conchology* (8): 126 ([Oahu]). Holotype MCZ 155950 figured by Johnson and Boss (1972, OPM **3**: 200, pl. 42, fig. 6).

dimorpha Gulick, *Achatinella*
1858, ALNHNY **6**: 236, pl. 8, fig. 56 (Oahu: Waimea, Pupukea, Waialea, and Kahuku). Holotype only, MCZ 39854 from Pupukea.

disjuncta Pilsbry and Cooke, *Nesopupa* (*Limbatipupa*) *newcombi*
1920, MofC (2) **25**: 317, 309, fig. 13 [actually figure 7] (Oahu: Mokuleia; Waianae Mts.). Holotype BPBM 17219; paratypes MCZ 78805.

dispersa Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Nesopupilla*)
1920, MofC (2) **25**: 284, pl. 27, figs. 7, 8 (Oahu: Makua). Holotype BPBM 11066; paratypes MCZ 180159.

dissotropis Ancey, *Helicina*
1904, PMSL **6**: 127, pl. 7, figs. 22, 23 (Oahu). Syntypes MCZ 191069.

distans Pease, *Helix*
1866, AJC **2**: 290 (Sandwich [Hawaiian] Islands). Not located in ANSP by Baker (1963) or elsewhere by Johnson (1994: 12).

diversa Gulick, *Achatinella*
1856, ALNHNY **6**: 220, pl. 7, figs. 42a, b (Oahu: Palolo, Waialae, Wailupe, and Niu). Holotype MCZ 39873 (fig. 41a) from Niu; paratype MCZ 39887 (fig. 42b is variety b) from Waialae.

dolei Baldwin, *Achatinella* (*Partulina*)
1895, PANSP **47**: 221, pl. 10, figs. 17, 18 (Maui: Honomanu). Figured holotype ANSP 65690a (fig. 17), *teste* Baker (1963: 194); paratypes ANSP 65690, MCZ 88551 and 119068.

dubia Newcomb, *Achatinella*
1853, ALNHNY **6**: 23 (Oahu); 1854, PZS **21**: 152 (preprint p. 26), pl. 24, fig. 65 (Oahu: Waianoe [Waianae]). Lectotype, here selected, BMNH 1992228/1 is the figured type; paralectotypes BMNH 1992228/2; CU 29953; MCZ 25797.

dubiosa C. B. Adams, *Achatinella tappaniana*
1851, *Contributions to Conchology* (8): 126 ([Maui]). Holotype MCZ 279303 figured by Johnson and Boss (1972, OPM **3**: 215, pl. 40, fig. 5).

dubitabilis Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Infranesopupa*)
1920, MofC (2) **25**: 291, pl. 28, fig. 9 (Molokai: Poholua, 2,500 feet elevation). Holotype BPBM 11068; paratypes MCZ 78797.

dulcis Cooke, *Leptachatina* (*Thaanumia*)
1911, MofC (2) **21**: 85, pl. 13, figs. 8, 10 (East Maui: Ulapalakua [Ulpalakua], Makawao). Holotype BPBM 12084; paratype MCZ 97627.

duoplicata Baldwin, *Laminella*
1908, *Nautilus* **22**: 68 (West Maui: Waichu Valley). Syntypes ANSP [no number] figured by Hyatt and Pilsbry (1911: 343, pl. 52, figs. 3–5); [holotype] ANSP 104692a (fig. 4), *teste* Baker (1963: 198); paratypes MCZ 97667.

duplocincta Pilsbry and Cooke, *Achatinella apexfulva*
1914, MofC (2) **22**: 323, pl. 55, figs. 6–8 ([Oahu]: "Wahiawa, Emerson, extinct?"). Figured syntype BPBM [no number] ex Cooke collection 1272 (fig. 8); figured syntypes MCZ 295306 (figs. 6, 7) ex Gulick collection 1213, from Oahu: Kawailoa, east side.

dwightii Newcomb, *Achatinella*
1855, ALNHNY **6**: 145 (Molokai); 1866, AJC **2**: 213, pl. 13, fig. 9. Lectotype, here selected, CU 29957A is the figured type, so marked; paralectotypes CU 29957; not in MCZ; not located in ANSP by Baker (1963).

eburnea Gulick, *Achatinella*
1856, ALNHNY **6**: 199, pl. 6, figs. 28a, b (East Maui: Honuaula). Holotype MCZ 39864 (fig. 28a); paratypes MCZ 39823, 136574, and 136575.

elegans Newcomb, *Achatinella*
1854, PZS **21**: 149 (preprint p. 23), pl. 24, fig. 57 (Oahu: Hauula). Lectotype, here selected, BMNH 1992189/1 is the "holotype" refigured by Welch (1958, PANSP **106**: 134, pl. 10, fig. 5); paralectotypes BMNH 1992189/2; CU 29959; MCZ 302450.

ellipsoidea Gould, *Achatinella*
1847, PBSNH **2**: 200 (Maui); 1852, USEE **12**: 87, pl. 7, figs. 96, 96a; 1862, *Otia Conch.*, p. 35. Holotype USNM 5498 refigured by Hyatt and Pilsbry (1911, MofC (2) **21**: 167, pl. 40, figs. 17, 18); paratype MCZ 156364.

elliptica Gulick [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 83, pl. 10, fig. 15 (Oahu: metropolis of the species is Waialei. It is also found in Kahuku and Hanula and rarely in Kawailoa). Holotype MCZ 39891; paratypes MCZ 302446; *both* from Waialei.

elongata Newcomb, *Achatinella*
1853, ALNHNY **6**: 26 (Oahu). Specimens identified by Newcomb [idiotypes] CU 29960; BPBM [no number], Garrett collection, ex Newcomb *teste* Hyatt and Pilsbry (1911: 231).

elongata Pease, *Succinea*
1870, JdeC **18**: 96 (Kauai). Lectotype MCZ 161665 selected by Johnson (1994, BMCZ **154**: 12, pl. 4, fig. 14).

emmersonii Newcomb, *Achatinella*
1854, PZS **21**: 156 (preprint p. 30), pl. 24, fig. 74 ([Oahu]: District of Waualua). Is *A. livida* Swainson, *teste* Newcomb (1858: 309). Lectotype, here selected, BMNH 1992235/1 is the figured type; paralectotype BMNH 1992235/2; not located in CU by Clarke (1960: 148); not in MCZ.

emortua Cooke, *Amastra* (*Amastrella*) *flavescens*
1917, BPBM *Occ. Pap.* **3**(3): 231, pl. A, fig. 6 (Hawaii: Huehue in the district of North Kona, on the northwestern slopes of Hualalai, about 1,700 feet elevation). Holotype and paratypes [listed as cotypes] BPBM 41971; paratype MCZ 97654.

eos Pilsbry and Cooke, *Amastra* (*Metamastra*)
1914, MofC (2) **23**: 26, pl. 2, figs. 14, 15 (Oahu: Keawaawa). Lectotype ANSP 108171a (fig. 15) selected by Baker (1963: 198); paralectotypes MCZ 31162.

erecta Pease, *Helicter* (*Laminella*)
1869, JdeC **17**: 174 (Maui). Holotype in MNHN figured by Fischer-Piette (1950, JdeC **90**: 73, fig. 53); paratypes MCZ 23338.

ernestina Baldwin, *Achatinella* (*Achatinellastrum*)
1895, PANSP **47**: 217, pl. 10, figs. 5, 6 (Oahu: Nuuanu Valley). Figured holotype ANSP 65706a (fig. 5), *teste* Baker (1963: 194).

errans Pilsbry and Cooke, *Partulina physa*
1913, MofC (2) **22**: 111, pl. 17, figs. 14–16 (Hawaii: near Pahoa, Puna [fig. 14]; Kaiwiki in the district of South Hilo [figs. 15, 16]). Lectotype ANSP 108205a (fig. 14) selected by Baker (1963: 194); paralectotypes MCZ 190897 from Puna.

euryomphala Ancey, *Tornatellina*
1889, BMSF **6**: 239 (West Maui: highest point). Holotype BPBM 18430, *teste* Pilsbry and Cooke (1915: 233); paratypes MCZ 165796.

evelynae Cooke and Kondo, *Carelia*
1952, BPBM *Occ. Pap.* **20**(20): 331, fig. 2, a–f (Kauai: Polihale, base of Polihale Ridge, 500 feet inland from ocean, 150 feet altitude; fossil). Holotype BPBM 9092; paratypes MCZ 187597.

exaequata Gould, *Helix* [*Microcystis*]
1846, PBSNH **2**: 171 (Kauai); 1852, USEE **12**: 47, pl. 5, figs. 61, 61a–c; 1856, *Ibid.*, Addenda and Corrigenda, p. 501; 1862, *Otia Conch.*, pp. 29, 243. Holotype USNM 5463; paratypes MCZ 87862 and 169134.

exilis Gulick, *Achatinella*

1856, ALNHNY **6**: 188, pl. 6, fig. 16 (Oahu: Keawaawa). Holotype MCZ 39827; paratypes MCZ 245206 and 136926.

expansa Pease, *Auriculella*
1868, JdeC **16**: 343, pl. 14, fig. 8 ([Maui]). Holotype in MNHN, *teste* Fischer-Piette (1950: 71); paratypes MCZ 45155.

explanata Gould, *Succinea* [*Omalonyx*]
1852, USEE **12**: 13, pl. 2, figs. 31, 31a–c (Kauai); 1862, *Otia Conch.*, p. 223. Holotype USNM 20870; paratypes MCZ 155126 and 169135.

extensa Pease, *Leptachatina*
1870, JdeC **18**: 92 (Kauai). Not mentioned by Fischer-Piette (1950: 74), or located by Johnson (1994: 12).

extincta Ancey, *Tornatellina*
1890, BSMF **7**: 341 (Maui [East Maui: Kaupakalua]). Syntypes, presumed to be in BPBM, mentioned by Pilsbry and Cooke (1915: 160) but not located by Cowie (personal communication); syntypes MCZ 175725.

fasciata Gulick, *Achatinella*
1856, ALNHNY **6**: 201, pl. 7, fig. 30 (Maui: Honukawai). Holotype MCZ 39849; paratypes MCZ 136570 and 136571.

fastigata Cooke, *Amastra* (*Amastrella*) *rugulosa*
1917, BPBM *Occ. Pap.* **3**(3): 229, pl. B, fig. 1 (Kauai: Koloa; Pleistocene). Holotype and 2 paratypes [listed as cotypes] BPBM 41997; paratypes MCZ 97593.

filocostata Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa perlonga*
1920, MofC (2) **25**: 262, pl. 23, fig. 12 (Kauai: Limahuli). Holotype BPBM 11057; paratypes MCZ 78766.

filocostata Pease, *Pityn*
1871, PZS for 1871: 454 (Kauai). Not located in BMNH, *teste* Mordan (personal communication), or elsewhere by Johnson (1994: 13).

flavescens Newcomb, *Achatinella*
1854, PZS **21**: 151 (preprint p. 25), pl. 24, fig. 62 (Hawaii). Lectotype, here selected, BMNH 1992262/1 is the figured type; paralectotypes BMNH 1992262/2; CU 29964; MCZ 141487 and 294945.

flavida Cooke [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 103, pl. 26, figs. 8, 9 (Molokai: Kamalo). Holotype [so labeled] BPBM 42390 (fig. 8); paratype ANSP 94495 (fig. 9); paratypes MCZ 97576.

flavidus Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 80, pl. 10, figs. 1, 1a (Oahu: metropolis is in Kalaikoa; it is also found in Ahonui). Holotype MCZ 39904 (fig. 1); paratype MCZ 302449 (fig. 1a is variety a); paratypes MCZ 147143–147145; *all* from Kalaikoa; paratypes MCZ 147146 from Ahonui.

flemingi Baldwin, *Partulina*
1906, *Nautilus* **19**: 111 (East Maui: Nahiku). Syntypes ANSP 110089 figured by Pilsbry and Cooke (1913, MofC (2) **22**: 70, pl. 19, figs. 5–11); [holotype] ANSP 110089a (fig. 10), *teste* Baker (1963: 194); [paratypes] MCZ 135726 and 135732.

formosa Gulick, *Achatinella*
1858, ALNHNY **6**: 235, pl. 8, fig. 55 (Oahu: Waimea). Holotype only, MCZ 39867.

fornicata Gould, *Helix*
1846, PBSNH **2**: 172 (Kauai); 1852, USEE **12**: 50; 1856, *Ibid.*, Addenda and Corrigenda, p. 501, "The shell which was described as *H. fornicata* has been unfortunately mislaid, and the figure numbered 64, where it was to be placed, represents *H. tongana* Quoy with its animal"; 1862, *Otia Conch.*, pp. 21, 243. Specimens subsequently identified by Gould [idiotypes] MCZ 169148.

fossilis Baldwin, *Amastra*
1903, *Nautilus* **17**: 35 (Hawaii: Palihoukapapa on the Hamakua slope of Mauna Kea, at an elevation of 4000 feet). Syntype Baldwin collection [no number] figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 315, pl. 47, fig. 10); syntypes BPBM 22346.

fossilis Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa lyrata*
1920, MofC (2) **25**: 237, pl. 19, figs. 7, 11 (Oahu: Manoa). Holotype BPBM 11039 (fig. 11); paratypes MCZ 78756.

fragilis Gulick, *Achatinella*
1856, ALNHNY **6**: 183, pl. 6, fig. 11 (Oahu: Punaluu). Holotype MCZ 39822 from Palolo [sic]; paratypes MCZ 45209 from Punaluu.

fragosa Cooke, *Amastra* (*Amastrella*)
1917, BPBM *Occ. Pap.* **3**(3): 236, pl. A, fig. 4 (Hawaii: Kapulehu, 3 miles north of Huehue; Pleistocene). Holotype BPBM 41976; paratype MCZ 97658.

fulgens Newcomb, *Achatinella*
1854, PZS **21**: 131 (preprint p. 4), pl. 22, fig. 24 (Oahu: Niu). Lectotype, here selected, BMNH 1992204/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992204/2; CU 29967; MCZ 25575, 25576 and 294981.

fulgida Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 12, pl. 2, figs. 39, 40 (West Maui: Mt. Lihua, Mt. Kukui, Akau-ka-imo, Ahoa; Thaanum). Figured holotype BPBM 12017; paratypes MCZ 202779 from Mt. Kukui ex Thaanum.

fulginosa Gould, *Achatinella*
1845, PBSNH **2**: 28 (Sandwich [Hawaiian] Islands); 1862, *Otia Conch.*, p. 96, ". . . is *Helix tristis* Férussac." Holotype MCZ 169194 figured by Johnson (1964, USNM *Bull.* **239**: 80, pl. 42, fig. 7).

fulvicans Baldwin, *Partulina*
1906, *Nautilus* **19**: 135 (East Maui: Kipahula Valley, Hana). Syntypes [no number] figured by Pilsbry and Cooke (1912, MofC (2) **22**: 73, pl. 19, figs. 15, 16); [holotype] ANSP 108212a [which type not indicated] *teste* Baker (1963: 194).

fumida Gulick, *Achatinella*
1856, ALNHNY **6**: 181, pl. 6, fig. 9 (Oahu: Waialei, Pupukea, Waimea, Kawailoa, and Helemanu [Helemano]). Holotype MCZ 39826; paratypes MCZ 40313, 45213, and 136940; *all* from Kawailoa; para-

types MCZ 45215 from Pupukea; paratypes MCZ 136938 from Helemano.

fumosa Newcomb, *Achatinella*
1854, PZS **21**: 140 (preprint p. 14), pl. 23, fig. 28 (Oahu: Manoa). Lectotype, here selected BMNH 1992245/1 is the figured type; paralectotypes BMNH 1992245/2; CU 29969; MCZ 142992 and 294982.

fusca Newcomb, *Achatinella*
1853, ALNHNY **6**: 28 (Oahu); 1854, PZS **21**: 145 (preprint p. 19), pl. 23, fig. 44 (Oahu: Manoa . . . near the base of the mountain at the head of Manoa valley). Lectotype, here selected, BMNH 1992255, is the "only specimen intact and suitable for lectotype designation," *teste* Naggs (personal communication); paralectotypes CU 29970; MCZ 142993.

fuscobasis Smith [in] Gulick and Smith, *Bulimella*
1873, PZS for 1873: 77, pl. 9, fig. 15 (Oahu: high up on Mount Kaala on the Mokuleia side). Holotype only, MCZ 39918, refigured by Pilsbry and Cooke (1913: 170, pl. 35, fig. 1).

fuscolineata Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 75, pl. 9, fig. 2 (Oahu: Kailua . . . varieties in nearly all the valleys between Palolo and Halawa). Lectotype, here selected, BMNH 1992200/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992200/2 and MCZ 159596; *all* from Kailua.

fuscospira Pilsbry and Cooke, *Partulina horneri*
1914, MofC (2) **22**: 365, pl. 54, fig. 13 (Hawaii: Kukuihaele). Figured holotype ANSP 111439a, *teste* Baker (1963: 194); paratypes MCZ 190893.

fuscozona Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 76, pl. 9, fig. 9 (Oahu: Makiki, two or three specimens have been found in Palolo). Holotype only, MCZ 39885 from Makiki.

fuscozonata Pilsbry and Cooke, *Partulina* (*Baldwinia*) *horneri*
1914, MofC (2) **22**: 365, pl. 17, figs. 2, 5 (Hawaii: Hamakua). Lectotype ANSP 65700a (fig. 2) selected by Baker (1963: 194); paralectotypes MCZ 65702.

fuscula Gulick, *Achatinella*
1856, ALNHNY **6**: 180, pl. 6, fig. 8 (Oahu: mountain forests of Mokuleia). Holotype only, MCZ 39814 from Palolo; specimen identified by Gulick [idiotype] MCZ 136932 from Lehui.

fusoidea Newcomb, *Achatinella*
1855, ALNHNY **6**: 144 (East Maui); 1866, AJC **2**: 213, pl. 13, fig. 8. Not located in CU by Clarke (1960: 149); not in MCZ; not located in ANSP by Baker (1963).

gamma Pilsbry and Cooke, *Helicina laciniosa*
1908, BPBM *Occ. Pap.* **3**(2): 202, fig. 3 (Oahu: Ewa, Wahiawa). Holotype BPBM 14902; paratype MCZ 191055; *both* from Ewa.

garrettiana Ancey, *Succinea*
1899, PMSL **3**: 272, pl. 12, fig. 7 (Hawaii: Hilo, Rainbow Falls). Holotype BPBM 19043; paratypes BPBM 18986 and MCZ 190648.

gentilis Cooke, *Amastra* (*Amastrella*) *conica*
1917, BPBM *Occ. Pap.* **3**(3): 233, pl. A, fig. 1 (Hawaii: Waikii station, land of Waikoloa, about 6,000 feet elevation). Holotype and paratypes [listed as cotypes] BPBM 41967; paratype MCZ 97657.

germana Newcomb, *Achatinella*
1854, PZS **21**: 151 (preprint p. 25), pl. 24, fig. 61 (Maui: Makawao). Lectotype, here selected, BMNH 1992225 is the figured and only type; paralectotypes CU 29971; not in MCZ.

gigantea Newcomb, *Achatinella*
1854, PZS **21**: 136 (preprint p. 10), pl. 22, fig. 17 (Maui: Haleakala). Lectotype, here selected, BMNH 1992244 is the figured and only type.

glabra Newcomb, *Achatinella*
1854, PZS **21**: 139 (preprint p. 13), pl. 22, fig. 25 (Oahu: Kolau poko). Lectotype BMNH 1992190/1 figured as the "holotype" selected by Welch (1954: 97, pl. 2, fig. 24); paralectotypes BMNH 1992190/2; CU 29972; MCZ 294941.

glauca Gulick, *Achatinella*
1858, ALNHNY **6**: 232, pl. 8, fig. 51 (Oahu: Kawailoa). Holotype only, MCZ 39855.

globuloidea Neal, *Pleuropoma laciniosa*
1934, BPBM *Bull.* **125**: 67, figs. 67, 68 (Kauai: Nonou Mountains, southwest side). Holotype BPBM 11214; paratypes MCZ 179709.

glossema Cooke, *Carelia*
1931, BPBM *Bull.* **85**: 80, pl. 15, figs. 1–3 (Kauai: Olokele). Holotype BPBM 86083; paratypes MCZ 97583.

gnampta Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Limbatipupa*) *newcombi*
1920, MofC (2) **25**: 317, 309, figs. 14, 15 [actually figs. 8, 8a] (Hawaii: Luakaha, Nuuanu). Holotype BPBM 12526; paratypes MCZ 78804.

gouldi Newcomb, *Achatinella*
1853, ALNHNY **6**: 21 (Maui: Wailuku Valley); 1854, PZS **21**: 129 (preprint p. 4), pl. 22, fig. 1. Lectotype, here selected, BMNH 1992202/1 is the figured type; paralectotypes BMNH 1992202/2; CU 29978; MCZ 294957.

gouldi Pilsbry and Cooke, *Lyropupa lyrata*
1920, MofC (2) **25**: 235, pl. 19, figs. 8, 9 ([Oahu]). Holotype MCZ 169464; paratypes MCZ 314964.

gracilis Pease, *Blauneria*
1860, PZS **28**: 145 (Sandwich [Hawaiian] Islands). Lectotype BMNH 1962770, selected by Kay (1965, *Bull.* BMNH *Zool.*, Suppl. 1: 26, pl. 9, fig. 3); paralectotypes MCZ 297790.

gracilis Pease, *Tornatellina*
1871, PZS for 1871: 460 (Kauai). Lectotype MCZ 50058, selected by Johnson (1994, BMCZ **154**: 15, pl. 4, fig. 10).

grana Newcomb, *Achatinella*
1853, ALNHNY **6**: 29 (East Maui); 1854, PZS **21**: 146 (preprint p. 20), pl. 23, fig. 46. Syntypes CU

29981; MCZ 142970 and 156308; not located in BMNH, *teste* Naggs (personal communication).

granifera Gulick, *Achatinella*
1856, ALNHNY **6**: 185, pl. 6, fig. 13 (Oahu: Keawaawa). Holotype MCZ 39830; paratypes MCZ 45216, 45217, 147017, and 147019.

grisea Newcomb, *Achatinella*
1854, PZS **21**: 153 (preprint p. 26), pl. 24, fig. 66 (Maui: Makawao). Lectotype, here selected, BMNH 1992229/1 [slightly damaged] is the figured type; paralectotype BMNH 1992229/2; paralectotypes CU 29983; MCZ 25869 and 25870; not included in list by Clarke (1960).

gulickiana Pilsbry and Cooke, *Achatinella* (*Achatinellastrum*) *lehuiensis*
1914, MofC (2) **22**: 273, pl. 42, fig. 4 (Oahu: Mokuleia, Waianae range). Holotype only, *teste* Pilsbry and Cooke, MCZ 30252, ex Gulick collection 1471.

gulickii Smith [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 78, pl. 9, fig. 17 ([Oahu]: most abundant in Kalaikoa and Ahonui but sometimes found in valleys to the west as far as Waialei). Holotype only, MCZ 39834 from Kalaikoa.

gummea Gulick, *Achatinella*
1856 ALNHNY **6**: 182, pl. 6, fig. 10 (Oahu: Mokuleia and Lihue). Holotype MCZ 39829; paratypes MCZ 45220, 136927, and 136928; *all* from Mokuleia; paratypes MCZ 45219 from Lihue.

guttula Gould, *Achatinella* [*Leptachatina*]
1847, PBSNH **2**: 201 (Maui); 1852, USEE **12**: 89, pl. 7, figs. 98, 98a; 1862, *Otia Conch.*, pp. 35, 244. Holotype USNM 5500; paratypes MCZ 142956 and 169182.

haena Cooke, *Laxisuccinea*
1921, BPBM *Occ. Pap.* **7**(12): 277, pl. 25, fig. 5 (Kauai: deposits in road cutting near the western extremity of the Haena Plain; Pleistocene or Recent). Holotype BPBM 58476; paratypes MCZ 97728.

haupuensis Cooke, *Godwinia*
1921, BPBM *Occ. Pap.* **7**(12): 267, pl. 24, fig. 3, text fig. 3 (Kauai: northern slope of Mount Haupu in the southeastern portion of the island). Holotype BPBM 58469; paratypes MCZ 97731.

hawaiiensis Ancey, *Lyropupa mirabilis*
1904, JofM **11**: 68, pl. 5, fig. 18 (Hawaii: Palihoukapapa, on the Hamakua slope of Mauna Kea, at an elevation of 4,000 feet). Holotype BPBM 18748, *teste* Cooke and Pilsbry (1920: 252); paratypes BPBM 36656 and MCZ 78762.

hawaiiensis Baldwin, *Achatinella* (*Partulina*)
1895, PANSP **47**: 225, pl. 10, figs. 24–26 (Hawaii: Hamakua). Figured holotype ANSP 65695a (fig. 24), *teste* Baker (1963: 194); paratypes MCZ 135755.

hawaiiensis Hyatt and Pilsbry, *Amastra* (*Amastrella*)
1911, MofC (2) **21**: 319, pl. 42, figs. 7, 8 (Hawaii: Waimanu; Baldwin). Lectotype ANSP 105540a (fig. 7) selected by Baker (1963: 198); paralectotypes MCZ 145766 from Baldwin collection 26 ex BSNH.

hayseldeni Baldwin, *Partulina*
1896, *Nautilus* **10**: 31 (Lanai). Syntypes ANSP [no number] figured by Pilsbry and Cooke (1913, MofC (2) **22**: 88, pl. 21, figs. 5–7); [holotype] ANSP 68872a [which type not indicated] *teste* Baker (1963: 194).

helena Newcomb, *Achatinella*
1853, ALNHNY **6**: 27 (Molokai); 1854, PZS **21**: 151 (preprint p. 25), pl. 24, fig. 63. Lectotype, here selected, BMNH 1992227/1 is the figured type, so marked; paralectotypes BMNH 1992227/2; CU 29988; MCZ 156044 and 294976.

heliciformis Ancey, *Amastra*
1890, BSMF **7**: 340 (Oahu: Waianae). Not mentioned by Pilsbry and Cooke (1914). Syntypes MCZ 147477.

helvina Baldwin, *Laminella* (*Laminella*)
1895, PANSP **47**: 227, pl. 11, fig. 30 (Molokai: Ohia Valley, near Kaluaaha). Figured holotype ANSP 65712a, *teste* Baker (1963: 198); paratypes MCZ 97662, 135752, 140237 and 191037.

henshawi Ancey, *Tornatellina*
1903 [1904], JdeC **51**: 299, pl. 12, figs. 9, 10 (Hawaii: Hamakua, Olaa). Not mentioned by Fischer-Piette (1950: 171); lectotype BPBM 18436 [18655 on plate caption] from Hamakua figured by Pilsbry and Cooke (1916: 264, pl. 55, fig. 3); paralectotypes MCZ 199562 from Hamakua.

henshawi Baldwin, *Amastra*
1903, *Nautilus* **17**: 34 (Hawaii: South Kona, altitudes from 1,800 to 4,000 feet). Syntype ANSP 104709 figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 318, pl. 47, fig. 15). Not found in ANSP by Baker (1963); syntypes MCZ 135767 and 138671.

henshawi Sykes, *Leptachatina*
1903, JofM **10**: 1, text fig. (Hawaii: Kona, 1,800 feet). Syntype BPBM 18853 figured by Cooke [in] Pilsbry and Cooke (1910, MofC (2) **21**: 86, pl. 1, fig. 15); syntypes MCZ 202696; not located in BMNH, *teste* Naggs (personal communication).

herbacea Gulick, *Achatinella*
1858, ALNHNY **6**: 233, pl. 8, fig. 52 (Oahu: forests between the streams of Waimea and Kawailoa). Holotype MCZ 39847; paratypes MCZ 40172; *both* from Kawailoa.

honomuniensis Pilsbry [in] Pilsbry and Cooke, *Newcombia cinnamomea*
1912, MofC (2) **22**: 12, pl. 14, figs. 6, 7 (Molokai: Honomuni). Holotype ANSP 110071a, *teste* Baker (1963: 194) [which type not indicated]; paratypes MCZ 190543.

horneri Baldwin, *Achatinella* (*Partulina*)
1895, PANSP **47**: 224, pl. 10, figs. 20–22 (Hawaii: [Kukuihaele], Hamakua). [Holotype] ANSP 65702a (fig. 20), *teste* Baker (1963: 194); paratypes MCZ 9456 and 190881.

humilis Newcomb, *Achatinella*
1855, ALNHNY **6**: 143 (Molokai: Kalai); 1866, AJC **2**: 211, pl. 13, fig. 4. Lectotype, here selected, CU

29989A is the figured type, so marked; paralectotypes CU 29989; MCZ 141451 and 294971; not located in ANSP by Baker (1963).

hutchinsonii Pease, *Helicter*
1862, PZS for 1862: 7 (Maui). Lectotype MCZ 45254 selected by Johnson (1994, BMCZ **154**: 15, pl. 4, fig. 2); paralectotype MCZ 141500.

hyattiana Pilsbry [in] Hyatt and Pilsbry, *Carelia*
1911, MofC (2) **21**: 108, pl. 21, figs. 1, 2 ([Kauai]). Figured holotype ANSP 10132, *teste* Baker (1963: 198); paratype MCZ 181217.

hybrida Newcomb, *Achatinella*
1854, PZS **21**: 147 (preprint p. 21), pl. 23, fig. 52 (Oahu: Kolau). Is *A. producta* Reeve, *teste* Newcomb (1858: 315). Lectotype, here selected, BMNH 1992268 is the figured and only type, *teste* Welch; not located in CU by Clarke (1960: 150), not in MCZ.

hyperleuca Pilsbry [in] Hyatt and Pilsbry, *Carelia bicolor*
1911, MofC (2) **21**: 114, pl. 20, figs. 5, 6 ([Kauai]). Lectotype ANSP 234432a (fig. 6) selected by Baker (1963: 198); paralectotypes MCZ 181216.

hystricella Cooke and Pilsbry [in] Pilsbry, *Pronesopupa* (*Pronesopupa*)
1920, MofC (2) **26**: 7, pl. 1, fig. 12 (Hawaii: Hilo, Reed's Island). Holotype BPBM 11032; paratypes MCZ 78813.

hystrix 'Mighels' Pfeiffer, *Helix*.
See under: *setigera* Gould, *Helix*, and as *Cookeconcha hystrix* (Pfeiffer, 1846), by Solem (1976: 220).

illibata Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellaria sykesii*
1916, MofC (2) **23**: 266, pl. 55, fig. 7 (Molokai: Kilohana, Puunea). Holotype BPBM 34028; paratypes [listed as cotypes] BPBM 24510 and ANSP 111859; paratype MCZ 97566.

illimis Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 10, pl. 10, fig. 3 (Oahu: Palehua in the Waianae Mts.). Holotype BPBM 12077; paratypes MCZ 191121.

induta Gulick, *Achatinella*
1856, ALNHNY **6**: 207, pl. 7, figs. 34a, e (Maui: Wailuku). Holotype MCZ 39821 (fig. 34a); paratype MCZ 39816 (fig. 34e is variety e); paratypes MCZ 136536 and 136539.

inopinata Cooke, *Amastra* (*Amastra*)
1933, BPBM *Occ. Paper* **10**(6): 23, pl. 2, figs. 11, 12 (East Maui: Kula, near the division of the lands of Keokea and Kamaole). Figured syntypes BPBM 10769; syntype MCZ 97650 from Keokea.

inornata Mighels, *Achatinella*
1845, PBSNH **2**: 21 (Oahu). Syntypes Jay collection [no number]. Listed by Jay (1850: 215) as a synonym of *Achatinella turritella* Férussac. Not located by Johnson (1949: 225), or subsequently.

intercarinata Mighels, *Helix*
1845, PBSNH **2**: 18 (Oahu). Not located by Johnson (1949: 226).

interjecta Hyatt and Pilsbry, *Amastra* (*Heteramastra*) *soror*
1911, MofC (2) **21**: 287, pl. 48, figs. 9–11 (West Maui: Lahaina). Lectotype ANSP 57827a (fig. 10) selected by Baker (1963: 198); paralectotypes MCZ 136894 and 136905 *both* ex Gulick collection.

intermedia Newcomb, *Achatinella*
1854, PZS **21**: 135 (preprint p. 9), pl. 22, fig. 13 (Oahu: Waianoe [Waianae]). Lectotype, here selected, BMNH 1992240/1 is the figured type; paralectotypes BMNH 1992240/2; CU 29990; MCZ 141437 and 294923.

interrupta Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Limbatipupa*) *newcombi*
1920, MofC (2) **25**: 315, 309, figs. 4a–6a (Hawaii: Waiaha). Holotype BPBM 42673 (fig. 5); paratypes MCZ 78806.

interrupta Pilsbry and Cooke, *Lyropupa perlonga*
1920, MofC (2) **25**: 261, pl. 22, fig. 5; pl. 25, figs. 1–4, 10 (Oahu: 1.5 miles west of Kahuku). Holotype ANSP 119446a (fig. 5) *teste* Baker (1963: 201); paratypes MCZ 78765.

irregularis Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 234, pl. 50, figs. 4–6 (West Maui: top of Mt. Kukui). Holotype BPBM 14157; paratypes [listed as cotypes] ANSP 111723; paratypes MCZ 97542.

isenbergi Cooke, *Carelia dolei*
1931, BPBM *Bull.* **85**: 53, pl. 6, figs. 6–12 (Kauai: Haena plain, a few hundred yards east of the Manoa stream). Holotype BPBM 37542a; paratype MCZ 97587.

johnsoni Hyatt and Pilsbry, *Amastra* (*Amastra*)
1911, MofC (2) **21**: 304, pl. 45, fig. 16 (West Maui: Wailuku). Holotype MCZ 136855 ex Gulick collection 1519.

johnsoni Newcomb, *Achatinella*
1854, PZS **21**: 147 (preprint p. 21), pl. 23, fig. 50 (Oahu: Kolau). Lectotype, here selected, BMNH 1992221 is the figured and only type, *teste* Welch; paralectotypes CU 29991; not in MCZ.

juddii Baldwin, *Achatinella* (*Achatinellastrum*)
1895, PANSP **47**: 216, pl. 10, figs. 3, 4 (Oahu: Halawa). Figured holotype ANSP 65709a (fig. 3), *teste* Baker (1963: 194).

juddii Pilsbry and Cooke, *Helicina*
1908, BPBM *Occ. Pap.* **3**(2): 208, fig. 13 (Kauai: Koloa Beach; fossil). Holotype BPBM 14898; paratypes MCZ 191117.

jugosa Mighels, *Helix*
1845, PBSNH **2**: 19 ([Kauai:] Waioli). Not located by Johnson (1949: 226).

juncea Gulick, *Achatinella*
1856, ALNHNY **6**: 230, pl. 7, fig. 49 (Oahu: Kalaikoa, Wahiawa, and Helemanu [Helemano]). Holotype only, MCZ 39842 from Wahiawa.

kaaeana Baldwin, *Partulina*
1906, *Nautilus* **19**: 113 (West Maui: Mt. Helu,

4,000 feet elevation). Syntypes ANSP [no number] figured by Pilsbry and Cooke (1912, MofC (2) **22**: 41, pl. 10, figs. 5–7); not located in ANSP by Baker (1963); syntype BPBM 51875; syntypes MCZ 190695.

kaalaensis Cooke and Pilsbry, *Nesopupa (Infranesopupa) dubitabilis*
1920, MofC (2) **25**: 292, pl. 28, fig. 13 (Oahu: Waianae Range at Mokuleia, and Kaala, eastern spur, about 2500 feet elevation). Holotype BPBM 11069 from Kaala; paratypes MCZ 180208.

kahakuloensis Pilsbry and Cooke, *Amastra baldwiniana*
1914, MofC (2) **23**: 43, pl. 8, figs. 5, 6 (West Maui: Kahakuloa; Thaanum). Lectotype ANSP 108168a (fig. 5) selected by Baker (1963: 198); paralectotypes MCZ 31177 and 183621 *both* ex Thaanum.

kahoolavensis Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 211, pl. 46, figs. 3, 4, 7 (Kahoolawe: Hakioawa). Holotype BPBM 36249; paratypes ANSP 111724 and MCZ 97521.

kahoolavensis Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 256, pl. 22, figs. 1–4, 8, 9 (Kahoolawe: Hakioawa). Holotype ANSP 108871a (fig. 1) *teste* Baker (1963: 201); paratypes MCZ 78769.

kahukuensis Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 208, pl. 46, figs. 11, 12 (Oahu: ledges near base of the "coral bluff," 1½ miles west of Kahuku). Holotype ANSP 112765a, *teste* Baker (1963: 194); paratypes MCZ 97513.

kailuanus Pilsbry and Cooke, *Tornatellides procerulus*
1915, MofC (2) **23**: 207, pl. 45, fig. 9 (Oahu: Kaelepulu, Kailua). Holotype ANSP 112766a, *teste* Baker (1963: 194); paratypes MCZ 97515.

kaipapauensis Welch, *Achatinella bulimoides*
1958, PANSP **110**: 162, pl. 11, figs. 14–16 (Oahu: Kaipapau, Hauula; Gulick). Holotype BPBM 10518 (fig. 15); paratypes MCZ 170103–170106 and 170027 (fig. 16).

kalalauensis Cooke, *Carelia*
1931, BPBM *Bull.* **85**: 32, pl. 3, figs. 1–8, 11–17 (Kauai: Kalalau, north side of valley east of double waterfall). Holotype BPBM 79947a (fig. 11); paratypes MCZ 190918.

kalamauensis Pilsbry and Cooke, *Amastra*
1914, MofC (2) **23**: 37, pl. 3, figs. 4–7 (Molokai: Kalamaula). Holotype ANSP 108227a (fig. 6) *teste* Baker (1963: 198); paratypes MCZ 97643 and 125304.

kalihiensis Pilsbry and Cooke, *Laminella gravida*
1915, MofC (2) **23**: 54, pl. 1, fig. 6 (Oahu: Kalihi). Holotype ANSP 109905a, *teste* Baker (1963: 198); paratypes MCZ 97660.

kaluaahacola Pilsbry and Cooke, *Partulina (Partulina) virgulata*
1914, MofC (2) **22**: 359, pl. 26, figs. 3, 3a (Molokai: Kaluaaha at about 1700 feet; Thaanum). Figured holotype ANSP 108194 selected as lectotype by Baker (1963: 195); paralectotypes MCZ 190628 ex Thaanum.

kamaloensis Pilsbry and Cooke, *Laminella depicta*
1915, MofC (2) **23**: 56; [figured but not described] 1911, MofC (2) **21**: pl. 52, figs. 6–8 (Molokai: northwestern Kamalo above the amphitheatre, along the old Kamalo ditch). Holotype ANSP 94494a (fig. 8), *teste* Baker (1963: 198); paratypes MCZ 31207, 191019, and 191921 *all* ex Thaanum.

kamaloensis Pilsbry and Cooke, *Partulina (Partulina) redfieldii*
1914, MofC (2) **22**: 362, pl. 26, figs. 4, 4a (Molokai: between the branch ravines above the Kamalo amphitheatre and below the old [Kamalo] irrigation ditch). Lectotype ANSP 108214a (fig. 4) selected by Baker (1963: 195); paralectotypes MCZ 190689.

kauaiensis Newcomb, *Achatinella*
1860, ALNHNY **7**: 145 (Kauai); 1866, AJC **2**: 209, pl. 13, fig. 1. Lectotype, here selected, CU 29992A is the figured type, so marked; paralectotypes CU 29992; MCZ 141331; and BMNH 1995102, ex MCZ 141331; not found in ANSP by Baker (1963).

kauaiensis Pease, *Melania*
1870, AJC **6**: 7, pl. 3, fig. 6 (Kauai). Holotype ANSP 26510, *teste* Baker (1964: 190); paratypes MCZ 74924.

kauensis Pilsbry and Cooke, *Amastra melanosis*
1915, MofC (2) **23**: 50, pl. 1, fig. 18 (Hawaii: Waiohinu, Kau). Lectotype ANSP 108147a selected by Baker (1963: 198); paralectotypes MCZ 31161 and 125298.

kaunakakaiensis Pilsbry and Cooke, *Amastra*
1914, MofC (2) **23**: 36, pl. 3, figs. 8–10 (Molokai: pipeline trail in upper Kaunakakai district, above and a short distance below the spring). Lectotype ANSP 108628a (fig. 10) selected by Baker (1963: 198); paralectotype MCZ 97603.

knudsenii Baldwin, *Amastra (Amastra)*
1895, PANSP **47**: 234, pl. 11, figs. 43, 44 (Kauai: Halemanu). Figured syntypes ANSP 65725; [holotype] ANSP 65725a [which type not indicated], *teste* Baker (1963: 198).

knudsenii Cooke, *Leptachatina (Leptachatina)*
1910, MofC (2) **21**: 8, pl. 9, figs. 11, 12 (Kauai: Waipo, near Halemanu, at an altitude of 3,500 feet). Holotype BPBM 12042; paratypes MCZ 202799.

kona Pilsbry and Cooke, *Lyropupa ovatula*
1920, MofC (2) **25**: 266, pl. 26, figs. 5, 10, 11, 14 (Hawaii: North Kona at Huehue). Holotype ANSP 44763a (figs. 10, 11, 14), *teste* Baker (1963: 201); paratypes MCZ 78772.

konana Pilsbry and Cooke, *Partulina (Baldwinia) physa*
1914, MofC (2) **22**: 365, pl. 54, figs. 5, 5a (Hawaii: North Kona at Honoula). Lectotype ANSP 111440a selected by Baker (1963: 195); paralectotypes MCZ 190896.

kuhnsi Cooke, *Amastra (Laminella)*
1908, BPBM *Occ. Pap.* **3**(2): 217, text fig. (West

Maui: Kahakuloa). Holotype BPBM 15142; paratype MCZ 97663.

kulinsi Pilsbry [in] Pilsbry and Cooke, *Partulina* (*Perdicella*)
1912, MofC (2) **22**: 22, pl. 14, figs. 8, 12–15 (West Maui: Honokohua). Lectotype ANSP 110057a (fig. 12) selected by Baker (1963: 195); paralectotypes MCZ 190583.

labiata Newcomb, *Achatinella*
1853, ALNHNY **6**: 27 (Oahu); 1854, PZS **21**: 141 (preprint p. 15), pl. 23, fig. 33 (Oahu: Lehui). Lectotype, here selected, BMNH 1992250/1 is the figured type; paralectotypes BMNH 1992250/2; CU 29993; MCZ 142994, 142998, and 294948.

laciniosa Mighels, *Helicina*
1845, PBSNH **2**: 19 (Oahu [Kauai: presumably the north coast near to, if not, Hanalei, Waioli; Cooke]). Lectotype MCZ 156497 selected by Johnson (1949, OPM **1**: 226, pl. 27, fig. 20).

lacrima Gulick, *Achatinella*
1856, ALNHNY **6**: 176, pl. 6, fig. 4 (Oahu: most from Lihue, but Kalaikoa, Wahiawa, Helemanu [Helemano] and Peula have each furnished one or two specimens). Holotype MCZ 39818 from "Lihue ?"; paratypes MCZ 147011–147013, *all* from Lihue; MCZ 147014 and 147015, *both* from Kalaikoa; MCZ 147016 from Helemano.

lactea Gulick, *Achatinella*
1856, ALNHNY **6**: 198, pl. 6, fig. 27 (Lanai). Holotype MCZ 39874; paratypes MCZ 136597.

laeva Baldwin, *Amastra* (*Laminella*)
1906, *Nautilus* **19**: 138 (East Maui: Haleakala Mt.). Syntypes ANSP [no number] figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 288, pl. 48, figs. 12–15); [holotype] ANSP 105556a [which type not indicated], *teste* Baker (1963: 198).

laevigata Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 11, pl. 6, figs. 3, 5 (Molokai: Mapulehu Ridge; Thaanum). Figured syntypes [in] BPBM 12025; syntypes MCZ 202812 ex Thaanum.

laevis Pease, *Leptachatina*
1870, JdeC **18**: 91 (Kauai); Crosse, 1876, JdeC **24**: 97, pl. 4, fig. 6. Holotype in MNHN, *teste* Fischer-Piette (1950: 149); paratypes MCZ 45173.

lagena Gulick, *Achatinella*
1856, ALNHNY **6**: 175, pl. 6, fig. 3 (Oahu: Helemanu [Helemano], Wahiawa, and Kalaikoa). Holotype MCZ 39810 labeled only as Oahu; paratypes MCZ 136930 from Helemano; MCZ 40309 and 136964–136967, *all* from Wahiawa; MCZ 136968 and 136969, *both* from Kalaikoa.

lahainana Pilsbry and Cooke, *Amastra*
1914, MofC (2) **23**: 43, pl. 6, figs. 1–10 (West Maui: Olowalu Gulch, District of Lahaina; Thaanum). Lectotype ANSP 113072a (fig. 1) selected by Baker (1963: 198); paralectotypes MCZ 31181 ex Cooke and 125275 ex Thaanum.

laminata Pease, *Helix*
1866, AJC **2**: 292 (Sandwich [Hawaiian] Islands); 1871, PZS for 1871: 474 as *Endodonta* (Kauai). Lectotype MCZ 17233 selected by Johnson (1994, BMCZ **154**: 16, pl. 3, fig. 4); paralectotypes MCZ 298477 and BPBM, *teste* MCZ label; not located in ANSP by Baker (1963: 232), or elsewhere by Solem (1976: 377).

lanaiensis Cooke [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 107, pl. 19, figs. 12–16 (Lanai). Holotype [so labeled] BPBM 42392; paratypes ANSP 92753 not located by Baker (1963); paratypes MCZ 31200 and 73052.

lanaiensis Cooke, *Leptachatina* (*Leptachatina*)
1911, MofC (2) **21**: 67, pl. 12, figs. 2, 3 (Lanai: [Koeli]; Thaanum). Holotype BPBM 12071; paratypes MCZ 97691 ex Cooke; paratypes MCZ 141579 and 202596 *both* ex Thaanum.

lanaiensis Cooke [in] Pilsbry and Cooke, *Lyropupa rhabdota*
1920, MofC (2) **25**: 241, pl. 20, fig. 6 (Lanai). Holotype BPBM 11041; paratypes MCZ 78750.

lanaiensis Pilsbry and Cooke, *Nesopupa* (*Nesopupilla*) *baldwini*
1920, MofC (2) **25**: 289, pl. 27, figs. 13–15 (Lanai). Holotype BPBM 34521; paratypes MCZ 78778.

lanceolata Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellina*
1916, MofC (2) **23**: 158, pl. 43, figs. 4–6 (Oahu: Nuuanu, Tantalus). Holotype BPBM 13442, *teste* Cooke and Kondo (1960 [1961]: 210); paratypes ANSP not located by Baker (1963); paratypes MCZ 97556.

lata C. B. Adams, *Achatinella dimondi*
1851, *Contributions to Conchology* (8): 127 ([Oahu]). Holotype MCZ 155954 figured by Johnson and Boss (1972, OPM **3**: 201, pl. 42, fig. 7).

lehuiensis Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 76, pl. 9, fig. 4 (Oahu: Lehui). Holotype only, MCZ 39876.

lemmoni Baldwin, *Partulina*
1906, *Nautilus* **19**: 112 (East Maui: Nahiku). Syntypes ANSP [no number] figured by Pilsbry and Cooke (1913, MofC (2) **22**: 61, pl. 12, figs. 19, 20); [holotype] ANSP 110081a [which type not indicated], *teste* Baker (1963: 195); [paratypes] MCZ 190797.

lepida Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 40, pl. 1, figs. 12, 13 (Hawaii: [Waimea Plains near] Mana; Thaanum). Holotype BPBM 12040; paratypes MCZ 202807.

leptospira Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 243, pl. 51, figs. 11–13 (Oahu: Nuuanu near the Pali). Holotype BPBM 36268; paratypes ANSP 111833 and MCZ 97540.

leucochila Gulick, *Achatinella*
1856, ALNHNY **6**: 173, pl. 6, fig. 1 (Kauai). Holotype only, MCZ 39820.

leucoderma Pilsbry and Cooke, *Laminella sanguinea*
1915, MofC (2) **23**: 55 (Oahu: near the middle of the western ridge of Popouwela, Waianae Mts.). Type not located in ANSP by Baker (1963); syntypes BPBM 35325 and MCZ 190991.

leucophaeus Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 82, pl. 9, fig. 16 (Oahu: Waialei). Holotype only, MCZ 39898.

leucorrhaphe Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 79, pl. 10, fig. 2 (Oahu: Kalaikoa). Holotype MCZ 39902; paratypes MCZ 147119 and 147121.

leucozonus Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 83, pl. 10, fig. 6 (Oahu: metropolis of this species is in Waialei. A few specimens have also been found in Wahiawa). Holotype only, MCZ 39906 from Waialei.

lignaria Gulick, *Achatinella*
1856, ALNHNY **6**: 209, pl. 7, fig. 35 (Maui: Wailuku). Holotype MCZ 39859; paratypes MCZ 136590, 136591, and 136593.

lilaceus Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 79, pl. 10, fig. 4 (Oahu: metropolis of the species is Ahonui. It is also abundant in Kalaikoa, but becomes very rare in Wahiawa, Helemano and Kawailoa). Holotype only, MCZ 39905 from Kalaikoa, refigured by Welch (1942: 137, pl. 10, fig. 8).

limbata Gulick, *Achatinella*
1858, ALNHNY **6**: 252, pl. 8, figs. 70a, b (Oahu: Ahonui and Kalaikoa). Syntypes MCZ 39884 (fig. 70a) and 39879 (fig. 70b), *both* from Ahonui.

lineolata Newcomb, *Achatinella*
1853, ALNHNY **6**: 29 (Maui); 1854, PZS **21**: 140 (preprint p. 14), pl. 23, fig. 29 (Hawaii). Lectotype, here selected, BMNH 1992246 is the figured and only type; paralectotypes CU 29996; not in MCZ.

littoralis Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Nesopupilla*)
1920, MofC (2) **25**: 283, pl. 28, fig. 1 (Oahu: Ewa). Figured syntype BPBM 11065; syntypes ANSP 44694, not mentioned by Baker (1963); syntypes MCZ 78779.

litus Pilsbry [in] Hyatt and Pilsbry, *Pterodiscus alatus*
1911, MofC (2) **21**: 122, pl. 22, figs. 4–6 (Lanai: [Koele Gulch]; Thaanum). Lectotype ANSP 94501a (fig. 4) selected by Baker (1963: 198); paralectotypes MCZ 190551 and 190552, *both* ex Thaanum.

longior Pilsbry [in] Pilsbry and Cooke, *Partulina* (*Partulina*) *terebra*
1912, MofC (2) **22**: 63, pl. 15, fig. 12 (West Maui: Wailuku, Gulick; Waiehu, Baldwin). Lectotype ANSP 92721a (fig. 12) selected by Baker (1963: 195); paralectotypes MCZ 136588 from Wailuku ex Gulick collection.

longiuscula Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 57, pl. 11, fig. 11 (Lanai; Thaanum). Holotype BPBM 12068; paratypes MCZ 202806 ex Thaanum.

luakahaense Cooke and Pilsbry [in] Pilsbry and Cooke, *Elasmias*
1915, MofC (2) **23**: 117, pl. 29, figs. 7–10 (Oahu: Nuuanu, Luakaha). Holotype BPBM 14145 from Luakaha; paratype MCZ 97553.

lucida Pease, *Leptachatina*
1870, JdeC **18**: 93 (Kauai). Not mentioned by Fischer-Piette (1950: 74), nor located by Johnson (1994).

lucidus Pease, *Melampus*
1869, AJC **5**: 75 (Oahu: [Honolulu]). Lectotype ANSP 22284 selected by Baker (1964: 151), figured by Johnson (1994, BMCZ **154**: 16, pl. 4, fig. 22); paralectotype ANSP 391058.

lumbalis Gould, *Succinea*
1846, PBSNH **2**: 183 (Kauai); 1852, USEE **12**: 17, pl. 2, figs. 18, 18a, b; (Hawaii: Mauna Kea); 1862, *Otia Conch.*, pp. 28, 244. Figured holotype USNM 5418; paratypes MCZ 169231.

luteostoma Baldwin, *Achatinella* (*Bulimella*)
1895, PANSP **47**: 217, pl. 10, figs. 7, 8 (Oahu: Palolo to Niu). Holotype ANSP 65704 (fig. 7), *teste* Pilsbry and Cooke (1913: 171); Baker (1963: 195) claims the [holotype] to be ANSP 65705a (fig. 8).

lymaniana Baldwin, *Achatinella* (*Bulimella*)
1895, PANSP **47**: 219, pl. 10, figs. 12, 13 (Oahu: Waianae Mts.). Lectotype BPBM 10420 (fig. 13), selected and refigured by Welch (1938, BPBM *Bull.* **152**: 129, pl. 13, fig. 2); paralectotypes BPBM 54934, MCZ 9464; not located in ANSP by Baker (1963).

lyonsiana Baldwin, *Achatinella* (*Bulimella*)
1895, PANSP **47**: 218, pl. 10, figs. 9–11 (Oahu: Konhuanui Mt., 3,000 feet above sea level). Figured syntypes ANSP 65693; [holotype] ANSP 65693a [which type not indicated], *teste* Baker (1963: 195); [paratypes] ANSP 65693.

lyrata Gould, *Pupa* [*Vertigo*]
1843, PBSNH **1**: 139 ([Oahu]); 1844, BJNH **4**: pl. 16, fig. 19; 1862, *Otia Conch.*, p. 189. Holotype MCZ 169233 refigured by Pilsbry and Cooke (1920, MofC (2) **25**: 233, pl. 19, fig. 4), also refigured by Johnson (1964, USNM *Bull.* **239**: 107, pl. 40, fig. 3); paratype MCZ 169234, also figured by Pilsbry and Cooke (fig. 5).

macromphala Ancey, *Tornatellina*
1903 [1904], JdeC **51**: 296, pl. 12, figs. 3, 4 (East Maui: Kaupakalua, Keanae; Oahu: Tantalus [near] Honolulu). Not mentioned by Fischer-Piette (1950: 171); syntypes BPBM 18439 mentioned by Pilsbry and Cooke (1915: 228); syntypes MCZ 199566 and 199567 *all* from Kaupakalua.

macroptychia Ancey, *Tornatellides*
1903 [1904], JdeC **51**: 305, pl. 12, figs. 20, 21 (Maui: Kaupakalua). Holotype BPBM 18437 [18438 on plate caption] refigured by Pilsbry and Cooke (1916: 239, pl. 51, fig. 8); paratype BPBM 36262 (*Ibid.*, fig. 7); paratypes ANSP 111835; paratypes MCZ 97544.

magna C. B. Adams, *Achatinella*
1851, *Contributions to Conchology* (8): 125 ([Lanai]). Holotype MCZ 155953 figured by Johnson and Boss (1972, OPM **3**: 208, pl. 42, fig. 10).

magnapustulata Cooke and Kondo, *Carelia paradoxa*
1952, BPBM *Occ. Pap.* **20**(20): 341, figs. 5a–c

(Kauai: Lepeuli). Holotype BPBM 9090; paratypes MCZ 187598.

mahogani Gulick, *Achatinella*
1858, ALNHNY **6**: 254, pl. 8, fig. 72 (Oahu: Ahonui and Kalaikoa). Holotype only, MCZ 39883 from Ahonui.

makawaoensis Pilsbry [in] Hyatt and Pilsbry, *Amastra* (*Amastra*)
1911, MofC (2) **21**: 294, pl. 43, figs. 7–9 (East Maui: Makawao). Lectotype ANSP 6707a (fig. 7) selected by Baker (1963: 198); paralectotype MCZ 97652.

malleata Ancey, *Auriculella*
1904, PMSL *16*: 120, pl. 7, fig. 12 (Oahu: Mt. Kaala [Waianae Mts.]). Holotype BPBM 18927, *teste* Cooke (1918: 293); paratype MCZ 73056.

malleata Smith [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 85, pl. 10, fig. 18 (East Maui: Kula). Holotype MCZ 39849; paratypes MCZ 136858 and 136861.

maniensis 'Newcomb' Pfeiffer, *Achatinella*
1856, PZS **23**: 207 (Mani [Maui]). *Laps. cal.* for *mauiensis*. Three syntypes BMNH 1996062 ex Cuming collection. *Achatinella mauiensis* Newcomb, 1866, AJC **2**: 217, pl. 13, fig. 6 (West Maui), emendation for *maniensis*; *Partulina maniensis* (Pfeiffer), Pilsbry and Cooke (1912: 20). Lectotype, here selected, CU 30013A is the type figured by Newcomb, so marked; paralectotypes CU 30013; not in MCZ; not located in ANSP by Baker (1963).

marginata Gulick, *Achatinella*
1856, ALNHNY **6**: 179, pl. 6, fig. 7 (Oahu: Kalaikoa). Holotype only, MCZ 39824.

mastersi Newcomb, *Achatinella*
1854, PZS **21**: 153 (preprint p. 27), pl. 24, fig. 67 (Mani [Maui]); 1858, ALNHNY **6**: 332 (Molokai, and is sparsely found on Maui). Lectotype, here selected, BMNH 1992263/1 is the figured type; paralectotypes BMNH 1992263/2; MCZ 142798 *all* from Maui. Specimens identified by Newcomb [idiotypes] CU 30012; MCZ 294940, *both* from Molokai.

mauiensis Newcomb, *Achatinella*
See under: *maniensis* 'Newcomb' Pfeiffer, *Achatinella*.

media Hyatt and Pilsbry, *Amastra* (*Metamastra*) *textilis*
1911, MofC (2) **21**: 167, pl. 30, figs. 11, 12 (Oahu: Aeia [Aiea], a short valley splitting the ridge northwest of Halawa). Holotype BPBM 72580; paratypes ANSP 104686 and MCZ 154726 ex BSNH 13378.

meineckei Cooke, *Amastra* (*Amastrella*) *anthonii*
1933, BPBM *Occ. Pap.* **10**(6): 14, pl. 1, figs. 7, 11–15 (Kauai: Kalalau, on the northern side of the valley, east of the double waterfall). Holotype BPBM 10764 (fig. 7); paratype MCZ 97597.

melanosis Newcomb, *Achatinella*
1854, PZS **21**: 144 (preprint p. 18), pl. 23, fig. 41 (Hawaii: [Mauna Loa]). Lectotype, here selected, BMNH 1992255 is the figured and only type, *teste* Naggs (personal communication); paralectotypes CU 30014; not in MCZ.

melanostoma Newcomb, *Achatinella*
1854, PZS **21**: 132 (preprint p. 6), pl. 22, fig. 7 (Oahu: Ewa). Lectotype, here selected, BMNH 1992208/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992208/2; MCZ 294946; not found in CU by Clarke (1960: 151).

metamorpha Pilsbry and Cooke, *Amastra* (*Cyclamastra*)
1914, MofC (2) **23**: 19, pl. 5, figs. 1–5 (West Maui: Olowalu Gulch; Thaanum). Lectotype ANSP 109835a (fig. 1) selected by Baker (1963: 198); paralectotypes MCZ 97609 ex Cooke and MCZ 31157 ex Thaanum.

micra Cooke, *Leptachatina* (*Leptachatina*) *brevicula*
1910, MofC (2) **21**: 24, pl. 8, fig. 55 (Kauai: Haleieie at 1,700 feet and Milolii at 1500 feet; Cooke). Holotype BPBM 12035; paratypes MCZ 97683 ex Cooke from Haleieie.

micra Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 263, pl. 23, fig. 7; pl. 25, figs. 5–7 (Oahu: Kaelepulu, Kailua). Holotype ANSP 48626a (fig. 5), *teste* Baker (1963: 202); paratypes MCZ 78764.

microstoma Gould, *Achatinella*
1845, PBSNH **2**: 28 ([Oahu]); 1862, *Otia Conch.*, p. 196, ". . . is *Helix textilis* Férussac." Lectotype MCZ 169244 selected by Johnson (1964, USNM *Bull.* **239**: 110, pl. 41, fig. 6); paralectotypes MCZ 169245.

microthauma Ancey, *Lyropupa*
1904, PMSL **6**: 126, pl. 7, fig. 20 (Oahu: Nuuanu Valley). Holotype BPBM 18750, *teste* Cooke and Pilsbry (1920: 238); paratypes MCZ 78754.

minuta Cooke and Pilsbry [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 90, pl. 25, figs. 5–9 (Oahu: Nuuanu, Palolo). Holotype [so labeled] BPBM 42377; paratypes ANSP [no number] and MCZ 73037 from Nuuanu.

modesta C. B. Adams, *Achatinella*
1851, *Contributions to Conchology* (8): 128 ([Molokai]). Lectotype MCZ 155951 selected by Johnson and Boss (1972, OPM **3**: 209, pl. 42, fig. 11); paralectotypes MCZ 156041.

moesta Newcomb, *Achatinella*
1854, PZS **21**: 157 (preprint p. 31), pl. 24, fig. 77 (Ranai [Lanai]). Lectotype, here selected, BMNH 1992265 is the figured and only type, *teste* Naggs (personal communication).

moloaensis Cooke and Kondo, *Carelia olivacea*
1952, BPBM *Occ. Pap.* **20**(20): 338, figs. 4, 4a–f (Kauai: Lepeuli Beach [and other localities]). Holotype BPBM 9091; paratypes MCZ 187595.

molokaiensis Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 22, pl. 10, figs. 11, 12 (Molokai: Mapulehu Ridge, Kaluaaha, and Wailau Pali; Thaanum). Holotype BMNH 12075; paratype MCZ 202818 from Kaluaaha ex Thaanum.

montana Baldwin, *Amastra*
1906, *Nautilus* **19**: 136 (West Maui: Mt. Kukui summit, 6,000 feet above sea level). Syntype ANSP [no number] figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 308, pl. 43, fig. 18); Figured holotype ANSP 113073a, *teste* Baker (1963: 198).

montana Cooke [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 82, pl. 27, fig. 9 (Oahu: Mt. Konahuanui, Lanihuli [unnamed variety]). Holotype ANSP 91819a, *teste* Baker (1963: 195); paratypes MCZ 73035 from Lanihuli.

moomomiensis Pilsbry and Cooke, *Amastra humilis*
1914, MofC (2) **23**: 38, pl. 7, figs. 9–14 (Molokai: Pleistocene of the sand dunes of Moomomi, around base of the bluff). Lectotype ANSP 110594a (fig. 9) selected by Baker (1963: 198); paralectotypes BPBM [no number] and MCZ 97640.

morbida Cooke, *Leptachatina* (*Thaanumia*)
1911, MofC (2) **21**: 87, pl. 13, fig. 12 (Molokai: Puu Kolekole; Thaanum). Holotype BPBM 12083; paratypes MCZ 202698 ex Thaanum.

mucida Baldwin, *Achatinella*
1895, PANSP **47**: 222, pl. 10, fig. 23 (Molokai: Makakupaia). Holotype ANSP 65708a, *teste* Baker (1963: 195).

mucronata Newcomb, *Achatinella*
1853, ALNHNY **6**: 28 (Molokai); 1854, PZS **21**: 146 (preprint p. 20), pl. 23, fig. 49 (Mani [Maui]). Lectotype, here selected, BMNH 1992258/1 is the figured type; paralectotypes BMNH 1992258/2; MCZ 141450 and 141460; *all* from Molokai. Specimens identified by Newcomb [idiotypes] CU 30019; MCZ 294949; *both* from Maui.

multilineata Newcomb, *Achatinella*
1854, PZS **21**: 138 (preprint p. 12), pl. 22, fig. 23 (Oahu: Kolau poco). Lectotype, here selected, BMNH 1992191/1 is the "holotype" refigured by Welch (1938, BPBM *Bull.* **152**: 19, pl. 1, fig. 2); paralectotype BMNH 1992191/2; four paralectotypes CU 30022 and 30023, with the note, "of the original lot of five specimens the one indicated by Newcomb is missing," Clarke (1960: 151) [as are all those described in the PZS]; paralectotype MCZ 294951.

multistrigata Pilsbry and Cooke, *Partulina* (*Partulina*) *theodorei*
1912, MofC (2) **22**: 34, pl. 9, figs. 12, 13, 16 (Molokai). Lectotype ANSP 109844a (fig. 12) selected by Baker (1963: 195) paralectotypes MCZ 133548.

multizonata Baldwin, *Achatinella* (*Achatinellastrum*)
1895, PANSP **47**: 215, pl. 10, figs. 1, 2 (Oahu: Nuuanu Valley). Figured syntypes ANSP 65703; [holotype] ANSP 65703a [which type not indicated], *teste* Baker (1963: 195); paratypes ANSP 65703 and MCZ 302448.

mustelina Mighels, *Achatinella*
1845, PBSNH **2**: 21 (Oahu: Waianai [Waianae]). Lectotype MCZ 156494 selected by Johnson (1949, OPM **1**: 227, pl. 27, fig. 10).

mutabilis Baldwin, *Partulina*
1908, *Nautilus* **22**: 68 (West Maui: Waichu Valley). Syntypes ANSP [no number] figured by Pilsbry and Cooke (1913, MofC (2) **22**: 68, pl. 20, figs. 1–7). Lectotype ANSP 110086a (fig. 1) selected by Baker (1963: 195).

nacca Gould, *Vertigo*
1862, PBSNH **8**: 280 (Hawaii); 1862, *Otia Conch.*, p. 237. Lectotype MCZ 169259 selected by Johnson (1964, USNM *Bull.* **239**: 114, pl. 42, fig. 2); paralectotypes MCZ 169260.

nana Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 232, pl. 11, figs. 48, 49 (Maui: Makawao). Figured [holotype] ANSP 65718a (fig. 49), *teste* Baker (1963: 198); [paratypes] ANSP 65718, MCZ 97651 and 135746.

nannodes Cooke, *Amastra* (*Heteramastra*)
1933, BPBM *Occ. Pap.* **10**(6): 26, pl. 2, fig. 16 (East Maui: Kula, near the division between the lands of Keokea and Kamaole). Figured syntype BPBM 10768; syntype MCZ 97615 from Keokea.

nattii 'Baldwin' Hartman, *Achatinella* (*Achatinellastrum*)
1888, PANSP **40**: 34, pl. 1, fig. 3 [as *nealii* on plate caption] (East Maui: Makawao). Syntypes MCZ 135756 and 135757 *both* from Baldwin ex BSNH; not found in ANSP by Baker (1963).

neckeri Cooke and Kondo, *Tornatellides* (*Aedituans*)
1960 [1961], BPBM *Bull.* **221**: 258, figs. 110a–f (Necker Island: Summit Hill). Holotype BPBM 8895; paratypes MCZ 187805 and 187806.

neglecta Pease, *Neritina*
1861, PZS **28**: 435 (Sandwich [Hawaiian] Islands). Lectotype BMNH 1961186 selected by Kay (1965, Bull. BMNH, Suppl. 1: 56, pl. 4, figs. 5, 6); paralectotypes MCZ 297789.

nematoglypta Pilsbry and Cooke, *Leptachatina*
1914, MofC (2) **23**: 14, pl. 9, figs. 9, 10 (Oahu: Halawa). Figured holotype ANSP 108322a, *teste* Baker (1963: 198); paratypes MCZ 202739 and 147043 from Kaeailoa ex Gulick collection mentioned in original description.

newcombii Lea, *Melania*
1856, PANSP **8**: 145 (Oahu); 1866, JANSP (2) **6**: 122, pl. 22, fig. 17; 1867, *Obs. Unio* **11**: 78, pl. 22, fig. 17. Holotype USNM 119620; paratypes USNM 119620a and 119703; paratypes MCZ 298287 from Newcomb ex Gould collection.

nigra Newcomb, *Achatinella*
1855, PBSNH **5**: 219 (East Maui); 1866, AJC **2**: 210, pl. 13, fig. 3. Lectotype, here selected, CU 30028A is the figured type, so marked; paralectotypes CU 30028; MCZ 142799 and 294954; and BMNH 1995103 ex MCZ 294954; not in ANSP (Baker, 1963).

nigrolabris Smith [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 85, pl. 10, fig. 9 (Oahu: metropolis of the species is Wahiawa; it is also found in all the valleys from Kalaikoa to Waimea). Lectotype, here selected, BMNH 1992381/1 is the fig-

ured type, so indicated; paralectotypes BMNH 1992381/2 and MCZ 136660 from Wahaiwa.

nitida Newcomb, *Achatinella*
1853, ALNHNY **6**: 29 (East Maui); 1854, PZS **21**: 140 (preprint p. 14), pl. 23, fig. 30. Lectotype, here selected, BMNH 1992247/1 is the figured type; paralectotypes BMNH 1992247/2; CU 30030; MCZ 45185, 142957, 294920, and 315849.

nivea Baldwin, *Achatinella* (*Partulina*)
1895, PANSP **47**: 222, pl. 10, fig. 19 (Maui: Makawao to Huelo). Figured holotype ANSP 65691a, *teste* Baker (1963: 196); paratypes MCZ 190771.

nivosa Newcomb, *Achatinella*
1854, PZS **21**: 132 (preprint p. 6), pl. 22, fig. 6 (Oahu: Niu). "Is universally admitted to be a scraped *A. abbreviata*," *teste* Pilsbry and Cooke (1913: 123). Lectotype, here selected, BMNH 1992207/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992207/2; not found in CU by Clarke (1960: 152); not in MCZ.

nubigena Pilsbry and Cooke, *Amastra* (*Heteramastra*)
1914, MofC (2) **23**: 48, pl. 5, figs. 11, 12; pl. 3, fig. 15 (West Maui: gulch to the right of Maunahoomaha, above Lahaina; Thaanum). Lectotype ANSP 109840a (pl. 5, fig. 11) selected by Baker (1963: 199); paralectotypes MCZ 141620 ex Thaanum.

nubilosa Mighels, *Achatinella*
1845, PBSNH **2**: 20 (Oahu [Molokai]). Lectotype MCZ 165606 selected by Johnson (1949, OPM **1**: 227, pl. 27, fig. 22); paralectotypes MCZ 156098.

nucleola Gould, *Achatinella*
1845, PBSNH **2**: 28 ([Kauai]); 1862, *Otia Conch.*, p. 196, ". . . is *Achatinella brevis* Pfeiffer." Lectotype MCZ 169265 selected by Johnson (1961, USNM *Bull.* **239**: 117, pl. 41, fig. 7); paralectotypes MCZ 169266.

nucula Smith [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 85, pl. 10, fig. 19 (probably Lanai). Holotype only, MCZ 38893.

nympha Gulick, *Achatinella*
1858, ALNHNY **6**: 251, pl. 8, fig. 69 (Oahu: Ahonui, Wahiawa, Helemanu [Helemano], Kawailoa, and Waimea). Holotype MCZ 39858 from Helemano; paratype MCZ 40099 from Ahonui.

oahuensis Cooke and Pilsbry, *Nesopupa* (*Limbatipupa*)
1920, MofC (2) **25**: 317, pl. 29, figs. 11, 12 (Oahu: Nuuanu Valley at Luakuha Falls). Holotype BPBM 11075; paratypes MCZ 78811.

oahuensis Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 222, pl. 48, figs. 8, 9 (Oahu: Kahuku). Holotype BPBM 14133; paratypes ANSP 111836 and MCZ 97516.

oahuensis Pilsbry and Cooke, *Helicina*
1908 BPBM *Occ. Pap.* **3**(2): 199, fig. 1 (Oahu: Waianae Mountains: back of Leilehua Ranch-house). Holotype BPBM 14911; paratypes MCZ 191100.

obesa Newcomb, *Achatinella*
1853, ALNHNY **6**: 24 (Maui: Hale-a-ka-la [Haleakala]); 1854, PZS **21**: 143 (preprint p. 17), pl. 23, fig. 39. Lectotype, here selected, BMNH 1992254/1 is the figured type; paralectotypes BMNH 1992254/2; MCZ 142800, 156036, and 294969. Specimens identified by Newcomb [idiotypes] CU 30038.

obliqua Gulick, *Achatinella*
1858, ALNHNY **6**: 245, pl. 8, fig. 63 (Oahu: Kahana). Holotype MCZ 39838; paratypes MCZ 40080, 170036, and 170042.

oblonga Pease, *Tornatellina*
1865, PZS for 1864: 673 (Islands of the Central Pacific); 1871, PZS for 1871: 473 (Tahiti). Lectotype MCZ 154941 selected by Johnson (1994, BMCZ **154**: 18, pl. 4, fig. 6); paralectotypes MCZ 297947. Found in the Hawaiian Islands *teste* Cooke and Kondo (1961: 196–209).

obscura Newcomb, *Achatinella*
1854, PZS **21**: 157 (preprint p. 31), pl. 24, fig. 78 (Ranai [Lanai]). Lectotype, here selected, BMNH 1992266/1 is the figured type; paralectotype BMNH 1992266/2; paralectotypes CU 30039; MCZ 142801 and 294937.

occidentalis Cooke, *Leptachatina* (*Leptachatina*) *nitida*
1910, MofC (2) **21**: 43, pl. 2, fig. 22 (West Maui: Maunahoomaha, Thaanum and Cooke; Lahaina, Baldwin). Figured holotype BPBM 12033; paratypes MCZ 97665 ex Cooke.

occidentalis Pilsbry and Cooke, *Partulina* (*Partulina*) *dwightii*
1914, MofC (2) **22**: 361, pl. 26, fig. 6 (Molokai: sand dunes of Moomomi, on the north coast almost due north of Mauna Loa; also summit of Mauna Loa). Holotype ANSP 108196a, *teste* Baker (1963: 196); paratypes MCZ 190672 from Mauna Loa.

octogyrata Gulick, *Achatinella*
1856, ALNHNY **6**: 190, pl. 6, fig. 18 (Oahu: Palolo Valley). Holotype MCZ 39819; paratypes MCZ 45224 and 136961.

olivacea Cooke [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 81, pl. 27, figs. 10, 11 (Oahu: Mt. Olympus at an elevation of about 2,500 feet, Konahuanui at an elevation of 3,000 [sic] feet). Figured holotype BPBM 42370; paratypes MCZ 31189 from Mt. Olympus.

olivacea Pease, *Carelia*
1866, AJC **2**: 293 (Sandwich [Hawaiian] Islands); 1871, PZS for 1871: 473 (Kauai). Holotype MCZ 57114, only specimen, *teste* Pease (1871a: 402), figured by Johnson (1994, BMCZ **154**: 19, pl. 2, fig. 14); two specimens subsequently identified by Pease [idiotypes] MCZ 23343 figured by Pilsbry and Cooke (1914, MofC (2) **23**: 16, pl. 9, figs. 11, 15).

oomorpha Gulick, *Achatinella*
1858, ALNHNY **6**: 246, pl. 8, fig. 64 (Oahu: Kahana). Holotype only, MCZ 39836.

orientalis Hyatt and Pilsbry, *Amastra reticulata*
1911, MofC (2) **21**: 181, pl. 29, figs. 8–11 (Oahu:

eastern range, Wahiawa; Gulick). Lectotype ANSP 92641a (fig. 8) selected by Baker (1963: 199) paralectotypes MCZ 136809 and 136810 ex Gulick collection 38, 1108

ornata Newcomb, *Achatinella*
1854, PZS **21**: 149 (preprint p. 23), pl. 24, fig. 55 (East Mani [Maui] . . . found in a limited locality in a deep ravine, at the back of Lahaina). Lectotype, here selected, BMNH 1992223/1 is the figured type; paralectotypes BMNH 1992223/2; CU 30042 [though labeled West Maui]; MCZ 25905 and 294922.

orycta Cooke and Pilsbry [in] Pilsbry, *Pronesopupa* (*Sericipupa*)
1920, MofC (2) **26**: 18, pl. 1, fig. 10 (Hawaii: Palihoukapapa; fossil). Holotype BPBM 11036; paratypes MCZ 180274.

oswaldi Welch, *Achatinella bulimoides*
1958, PANSP **110**: 170, pl. 13, figs. 1, 1a, b, 2, 17, 17a, b (Oahu: Kahana–Punaluu Ridge). Holotype ANSP 192589 (fig. 2); paratypes MCZ 170019 (figs. 17, 17a, b).

ovata Newcomb, *Achatinella*
1853, ALNHNY **6**: 22 (Oahu: Waiauai [Waianae]); 1854, PZS **21**: 130 (preprint p. 4), pl. 22, figs. 2, 2a (Oahu: Kahana, Koolan [Koolau]). Lectotype BMNH 1992193/1 is the figured type (fig. 2), selected and refigured by Welch (1958, PANSP **110**: 186, pl. 14, fig. 8); paralectotype BMNH 1992193/2 (fig. 2a); paralectotypes BMNH 1992193/3; CU 30044; MCZ 294977 and 315852.

ovatula Cooke, *Amastra* (*Amastrella*)
1933, BPBM *Occ. Pap.* **10**(6): 17, pl. 2, figs. 5–7 (Kauai: Pleistocene deposits near the western edge of the Haena plain, deposits of similar age at Limahuli). Syntypes BPBM 10758 and 37537; syntype MCZ 97598 from Haena.

ovatula Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 265, pl. 23, fig. 11; pl. 24, figs. 1–5 (Oahu: Kaelepulu, Kailua). Holotype ANSP 119434 (figs. 1–3) not mentioned by Baker (1963); paratypes MCZ 78777 and 180280.

pachystoma Pease, *Helicter* (Labiella)
1869, JdeC **17**: 171 (Kauai). Measured holotype in MNHN, *teste* Fischer-Piette (1950, JdeC **90**: 73, fig. 52); paratypes MCZ 45181.

pagodula Cooke, *Amastra* (*Amastrella*)
1917, BPBM *Occ. Pap.* **3**(3): 237, pl. B, fig. 4 (Hawaii: Pleistocene at Huehue about 1000 feet elevation, Puwaawaa). Holotype [in] BPBM 41974; paratype MCZ 97653, *all* from Huehue.

papyracea Gulick, *Achatinella*
1856, ALNHNY **6**: 229, pl. 7, fig. 48 (Oahu: Kalaikoa, Ahonui, and Wahiawa). Holotype only, MCZ 39865 from Kalaikoa.

parvula Gulick, *Achatinella*
1856, ALNHNY **6**: 195, pl. 6, fig. 24 ([Maui]). Holotype only, MCZ 39815.

patula Mighels, *Succinea*
1845, PBSNH **2**: 21 (Oahu). Not located by Johnson (1949: 227).

paucicostatus Pease, *Pithys*
1871, JdeC **18**: 395 (Kauai). Lectotype MCZ 17271 selected by Johnson (1994, BMCZ 154: 20, pl. 2, fig. 7); paralectotypes MCZ 298476; not mentioned by Fischer-Piette (1950: 76).

paulula Cooke, *Amastra* (*Metamastra*)
1917, BPBM *Occ. Pap.* **3**(3): 240, pl. B, fig. 6 (Oahu: Pleistocene of Malaikahana). Holotype [in] BPBM 41982; paratypes MCZ 97625.

pauxillus Gould, *Helix*
See under: *pusillus* Gould, *Helix*.

pellucida Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 231, pl. 11, figs. 41, 42 (Oahu: Waianae Valley). Holotype ANSP 65721a (fig. 41), *teste* Baker (1963: 199).

pellucida Pilsbry and Cooke, *Auriculella auricula*
1915, MofC (2) **23**: 80, pl. 24, fig. 10 (Oahu: Kaliuwaa, Punaluu, and Hauula). Figured holotype ANSP 92503a, *teste* Baker (1963: 196) from Kaliuwaa; paratypes MCZ 40319, 159523 and 159524 *all* from Kaliuwaa and 159519 from Hauula, *all* ex Gulick collection.

peponum Gould, *Pupa* [*Tornatellina*] [*Leptinaria*]
1847, PBSNH **2**: 197 ([Hawaii: Hilo; Oahu]); 1852, USEE **12**: 93, pl. 7, figs. 104, 104a–e; 1862, *Otia Conch.*, pp. 34, 244. Holotype USNM 5506 refigured by Pilsbry and Cooke (1915, MofC (2) **23**: 157, pl. 35, figs. 1, 2); paratypes MCZ 175724 and 216798.

perantiqua Cooke and Kondo, *Partulina dubia*
1952, BPBM *Occ. Pap.* **20**(20): 344, fig. 6c (Oahu: Kahuku Point). Holotype BPBM 9094; paratypes MCZ 187614.

percostata Pilsbry and Cooke, *Lyropupa micra*
1920, MofC (2) **25**: 264, pl. 25, figs. 11, 12 (Oahu: Kaelepulu, Kailua). Figured holotype ANSP 48627a, *teste* Baker (1963: 202); paratypes MCZ 78773.

perlonga Pease, *Vertigo*
1871, PZS for 1871: 462 (Oahu: [Nuuanu]). Holotype MCZ 48063 figured by Pilsbry and Cooke (1920, MofC (2) **23**: 258–259, pl. 23, figs. 1, 2).

perkinsi Sykes, *Newcombia*
1896, PMSL **2**: 130 (Molokai: Molokai Mountains; Perkins); 1900, *Fauna Hawaiiensis* **2**(4): 332, pl. 11, fig. 36. Lectotype, here selected, BMNH 1900.12.18.1468 is the figured type, so labeled; paralectotypes BMNH 1900.12.18.1469–1487 and MCZ 135503 ex Sykes.

perpusilla Smith [in] Gulick and Smith, *Auriculella*
1873, PZS for 1873: 87, pl. 10, fig. 26 (Oahu: Kahalu). Holotype only, MCZ 39912 [fragment].

perversa Cooke [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 90, pl. 25, figs 3, 4 (Oahu: Nuuanu, Kuliouou). Holotype BPBM 42384; paratypes MCZ 73044; *both* from Nuuanu.

petila Gulick, *Achatinella*
1856, ALNHNY **6**: 189, pl. 6, fig. 17 (Oahu: Koko). Holotype MCZ 39813; paratype MCZ 245227.

petricola Newcomb, *Achatinella*
1855, ALNHNY **6**: 143 (Molokai); 1866, AJC **2**: 211, pl. 13, fig. 6 (on the rocky sides of a Oali or precipice). Lectotype, here selected, CU 30069A appears to be the figured type; paralectotype CU 30069; not in MCZ; not found in ANSP by Baker (1963).

pexa Gulick, *Achatinella*
1856, ALNHNY **6**: 197, pl. 6, fig. 26 ([Oahu]). Holotype only, MCZ 39870, refigured by Pilsbry and Cooke (1913: 116, pl. 26, fig. 12; pl. 50, fig. 18).

pfeifferi Newcomb, *Achatinella*
1853, ALNHNY **6**: 25 (Molokai); 1854, PZS **21**: 150 (preprint p. 24), pl. 24, fig. 58. Syntypes MCZ 25906, 156039, and 294935; not located in BMNH by Naggs (personal communication); not found in CU by Clarke (1960: 153).

phaeostoma Ancey, *Partulina physa*
1904, PMSL **16**: 121 ([Hawaii: 2 miles from Mana]). "Type" BPBM 18819, *teste* Pilsbry and Cooke (1913: 107); paratypes MCZ 190882.

phaeozona Gulick, *Achatinella*
1856, ALNHNY **6**: 214, pl. 7, fig. 40 (Oahu: Keowaawa). Holotype MCZ 242163; paratype MCZ 241423 figured by Pilsbry and Cooke (1914: 184, pl. 24, fig. 11).

physa Newcomb, *Achatinella*
1854, PZS **21**: 152 (preprint p. 26), pl. 24, fig. 64 (Hawaii: Mouna [Mauna] Kea); 1855, PBSNH **5**: 218, "immature state"; 1866, AJC **2**: 214, pl. 13, fig. 10. Lectotype, here selected, CU 30072A is the figured type, so marked; paralectotypes CU 30072 and 30073; MCZ 154793 and 294980; not located in BMNH by Naggs (personal communication); not found in ANSP by Baker (1963).

picta Mighels, *Achatinella*
1845, PBSNH **2**: 21 (Oahu [Maui]). Lectotype MCZ 176982 selected by Johnson (1949, OPM **1**: 228, pl. 27, fig. 19); paralectotypes MCZ 165608.

pilsbryi Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 55, pl. 11, figs. 5, 6 (Oahu: Kukaeiole in Kaaawa). Holotype BPBM 12072; paratypes MCZ 97707 and 202368.

pilsbryi Cooke, *Tornatellides*
1914, *Nautilus* **28**: 79 (Oahu: Popouwela, in the Waianae Mts.); [in] Pilsbry and Cooke, 1915, MofC (2) **23**: 221, pl. 48, figs. 5–7. Holotype BPBM 36261; paratypes [listed as cotypes] ANSP 111838 and 110764; paratype MCZ 97514.

platystyla Gulick, *Achatinella*
1856, ALNHNY **6**: 196, pl. 6, fig. 25 (Oahu: Kawailoa). Holotype only, MCZ 39839, refigured by Pilsbry and Cooke (1913: 116, pl. 26, fig. 11; pl. 50, fig. 17).

plicata 'Mighels' Pfeiffer, *Achatinella*
1848, *Monographia Heliceorum Viventium* **2**: 235 (Molokai). The type figured by Reeve (1850, *Conchologia Iconica 6, Achatinella*: pl. 6, species 44) not located in BMNH by Naggs (personal communication); not located by Johnson (1949: 228).

plicifera Ancey, *Nesopupa*
1904, PMSL **6**: 122, pl. 7, fig. 14 (Oahu: Nuuanu Valley). Holotype BPBM 18703, *teste* Cooke and Pilsbry (1920: 280); paratypes MCZ 9646.

plumata Gulick, *Achatinella*
1856, ALNHNY **6**: 217, pl. 7, fig. 41 (Oahu: Niu, Wailupe, Waialae, Palolo, and Kailua). Holotype MCZ 159597 from Waialae; paratypes MCZ 159612 and 159613; *both* from Niu.

plumbea Gulick, *Achatinella*
1856, ALNHNY **6**: 213, pl. 7, fig. 39 (East Maui: Kula). Holotype MCZ 39832; paratypes MCZ 136520 and 136522.

pluscula Cooke, *Amastra* (*Cyclamastra*) *umbilicata*
1917, BPBM *Occ. Pap.* **3**(3): 228, pl. C, fig. 2 (Hawaii: Kapulehu, in the district of North Kona, about 18,000 feet [sic] elevation). Holotype and paratypes [listed as cotypes] BPBM 41978; paratypes MCZ 97600.

polita Newcomb, *Achatinella*
1853, ALNHNY **6**: 24 (Molokai); 1854, PZS **21**: 142 (preprint p. 16), pl. 23, fig. 37. Lectotype, here selected, BMNH 1992215/1 is the figured type; paralectotypes BMNH 1992215/2; CU 30077; MCZ 25845 and 294964.

polymorpha Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 81, pl. 10, fig. 5 (Oahu: typical forms are found in Waipio and Wahiawa. Varieties are sometimes found in Kalaikoa and Ahonui). Holotype MCZ 39901; paratypes MCZ 147167–147169; *all* from Waipio.

porcellana Newcomb, *Achatinella*
1854, PZS **21**: 146 (preprint p. 20), pl. 23, fig. 47 (East Maui). Lectotype, here selected, BMNH 1992219 is the figured and only type; paralectotypes MCZ 25859; not found in CU by Clarke (1960: 153).

porphyrea Newcomb, *Achatinella*
1854, PZS **21**: 136 (preprint p. 10), pl. 22, fig. 16 (Oahu: Waianoe [Waianae]). Lectotype, here selected, BMNH 1992243/1 is the figured type; paralectotypes BMNH 1992243/2; CU 30078; MCZ 294970.

porphyrostoma Pease, *Helicter* (*Amastra*)
1869, JdeC **17**: 172 (Oahu). Two syntypes MCZ 45256, one of which was figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 226, pl. 37, fig. 13).

porrecta Mighels, *Paludina*
1845, PBSNH **2**: 22 (Oahu). Not located by Johnson (1949: 228).

prasinus Reeve, *Achatinella*
1850, *Conchologia Iconica 6, Achatinella*: pl. 4, species 27 ([Hawaiian Islands]; Cuming collection). Lectotype, here selected, BMNH 1992198/1 is the figured type; paralectotypes BMNH 1992198/2; MCZ 298282 ex Cuming.

prisca Ancey, *Lyropupa magdalenae*
1904, JofM **11**: 68, pl. 5, fig. 19 ([Hawaii: Mana; Pleistocene]). Holotype BPBM 18746, *teste* Cooke and Pilsbry (1920: 244); paratypes MCZ 180232.

problematica Cooke, *Amastra* (*Cyclamastra*)
1933, BPBM *Occ. Pap.* **10**(6): 9, pl. 1, fig. 5 (Oahu:

Kawailoa [and several other localities]). Holotype BPBM 10772; paratype MCZ 97616.

procerula Ancey, *Tornatellina*
1903 [1904], JdeC **51**: 302, pl. 12, figs. 13, 14 (Maui: Kaupakalua). Lectotype BPBM 36246 selected by Pilsbry and Cooke (1915, MofC (2) **23**: 205, pl. 45, figs. 4, 5); paralectotypes MCZ 75389.

producta Mighels, *Physa*
1845, PBSNH **2**: 21 (Oahu). Not located by Johnson (1949: 228).

producta Reeve, *Achatinella*
1850, *Conchologia Iconica 6, Achatinella*: pl. 2, species 13 (Sandwich [Hawaiian] Islands; Cuming collection). Lectotype, here selected, BMNH 1992197/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992197/2; MCZ 298283 ex Cuming.

proximus Pease, *Helicter*
1862, PZS for 1862: 6 (Molokai). Lectotype MCZ 25823 selected by Johnson (1994, BMCZ **154**: 21, pl. 4, fig. 1).

pulchra Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 29, pl. 10, figs. 7, 8 (Oahu: Waianae Mts. back of Leilehua). Holotype BPBM 12078; paratype MCZ 97696.

pulchra Pease, *Auriculella*
1868, JdeC **16**: 346, pl. 14, fig. 6 ([Oahu]). Holotype and four paratypes in MNHN, *teste* Fischer-Piette (1950: 71); paratypes MCZ 161609.

pullata Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 228, pl. 11, figs. 31, 32 (Molokai: Waikolu). Figured syntypes ANSP 65715; [holotype] ANSP 65715a [which type not indicated], *teste* Baker (1963: 199); [paratypes] MCZ 47228.

pumicatus Mighels, *Bulimus*
1845, PBSNH **2**: 19 (Oahu [Kauai]). Lectotype MCZ 177002 selected by Johnson (1949, OPM **1**: 228, pl. 27, fig. 13); paralectotypes MCZ 156033.

pupoidea Cooke, *Leptachatina*
1911, MofC (2) **21**: 74, pl. 7, figs. 43, 44 (Kauai: Milolii at 1,500 feet). Holotype BPBM 12009; paratypes MCZ 97679.

pupoidea Newcomb, *Achatinella*
1854, PZS **21**: 144 (preprint p. 18), pl. 23, fig. 42 (East Maui). Lectotype, here selected, BMNH 1992256/1 is the figured type; paralectotypes BMNH 1992256/2; CU 30086, *all* labeled as from West Maui; MCZ 294967.

pusilla Newcomb, *Achatinella*
1855, ALNHNY **6**: 144 (Ranai [Lanai]); 1866, AJC **2**: 211, pl. 13, fig. 6. Lectotype, here selected, CU 30087A appears to be the figured type; paralectotypes CU 30087; MCZ 294974; not in ANSP (Baker, 1963).

pusillus Gould, *Helix*
1846, PBSNH **2**: 171 ([East] Maui: mountains); 1852, USEE **12**: 40, pl. 3, figs. 46, 46a–c. Not *Helix pusillus* Vallot, 1803; Lowe, 1831; Sachi, 1832; Roemer, 1839; or Pfeiffer, 1839; changed to: *Helix pauxillus* Gould; 1862, *Otia Conch.*, pp. 19, 243. Holotype USNM 20964.

puukolekolensis Pilsbry and Cooke, *Lyropupa kahoolavensis*
1920, MofC (2) **25**: 258, pl. 26, figs. 9, 12 (Molokai: Puukolekole). Lectotype ANSP 119475 (fig. 9) selected by Baker (1963: 202); paralectotypes MCZ 78771.

pygmaea Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 75, pl. 9, fig. 11 (Oahu: Waipio). Holotype only, MCZ 39881.

pyramidalis Gulick, *Achatinella*
1856, ALNHNY **6**: 204, pl. 7, fig. 32 (Maui: Lahaina). Holotype MCZ 39861; paratypes MCZ 136541.

pyramis Pfeiffer, *Achatinella*
1846, PZS **13**: 90 (Sandwich [Hawaiian] Islands); Reeve, 1850, *Conchologia Iconica 6, Achatinella*: pl. 6, species 41. Lectotype, here selected, BMNH 1992237/1 is the figured type [damaged]; paralectotypes BMNH 1992237/2; MCZ 298250 ex Cuming.

quadrata Ancey, *Succinea*
1904, PMSL **6**: 119, pl. 7, fig. 5 (Hawaii: Olaa, Kaiwiki, 2,550 feet above sea level). Holotype BPBM 18994; paratypes MCZ 190645.

radiata Gould, *Achatinella*
1845, PBSNH **2**: 27 ([Maui]); 1862, *Otia Conch.*, p. 195. Not located in Gould "type" collection by Johnson (1964, USNM *Bull.* 239: 138). Syntypes MCZ 298281 ex Gould collection.

recta Newcomb, *Achatinella*
1854, PZS **21**: 145 (preprint p. 19), pl. 23, fig. 45. Lectotype, here selected, BMNH 1992218/1 is the figured type, *teste* Welch; paralectotype BMNH 1992218/2; not found in CU by Clarke (1960: 153); not in MCZ.

redfieldi Newcomb, *Achatinella*
1853, ALNHNY **6**: 22 (Mani [Maui]: Wailuku); 1854, PZS **21**: 131 (preprint p. 6), pl. 22, fig. 5 (Molokai and East Maui). Lectotype, here selected, BMNH 1992206/1 is the figured type from [Molokai: Makakupia]; paralectotypes BMNH 1992206/2; CU 30091; MCZ 294921 from Molokai.

reevei C. B. Adams, *Achatinella*
1851, *Contributions to Conchology* (8): 128. New name for *Achatinella viridans* Reeve, non Mighels 1845.

remyi Newcomb, *Achatinella*
1855, ALNHNY **6**: 146 (Ranai [Lanai]); 1866, AJC **2**: 215, pl. 13, fig. 13. Lectotype, here selected, CU 30093A is the figured type, so marked; paralectotype CU 30093; not in MCZ; not in ANSP (Baker, 1963).

resinula Gulick, *Achatinella*
1856, ALNHNY **6**: 174, pl. 6, fig. 2 (Oahu: Kawailoa, Waimea, Pupukea, Waialei, and Punaluu). Holotype MCZ 39812; paratypes MCZ 136951 and 136952; *all* from Kawailoa.

reticulata Gould, *Physa*
1847, PBSNH **2**: 214 (Sandwich [Hawaiian] Is-

lands); 1852, USEE **12**: 118, pl. 9, figs. 140, 140a–b; 1862, *Otia Conch.*, p. 43. Holotype USNM 4440 [badly broken]; paratypes USNM 20710 and MCZ 216780.

reticulata Newcomb, *Achatinella*
1854, PZS **21**: 148 (preprint p. 22), pl. 24, fig. 54 (Oahu: Waianoe [Waianae]). Lectotype, here selected, BMNH 1992260/1 is the figured type; paralectotypes BMNH 1992260/2; CU 30095; MCZ 294962.

rhabdota Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 239, pl. 20, fig. 2 (Molokai: Pelekunu). Holotype BPBM 11040; paratypes MCZ 78752.

rhadina Cooke and Pilsbry, *Nesopupa* (*Nesodagys*) *wesleyana*
1920, MofC (2) **25**: 301, pl. 29, fig. 13 (Molokai: Poholua). Holotype BPBM 11083; paratypes MCZ 78793.

rigida Hyatt [in] Hyatt and Pilsbry, *Carelia*
1911, MofC (2) **21**: 111, pl. 21, figs. 8, 13 (Kauai). Holotype BPBM 73841; paratypes MCZ 88147 ex BSNH.

ronaldi Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 234, pl. 50, figs. 7, 8 (Oahu: Palehua in the Waianae Mts.). Holotype BPBM 36267; paratypes ANSP 111844 and MCZ 97539.

rosealimbata Welch, *Achatinella bulimoides*
1954, PANSP **106**: 73, pl. 1, figs. 9–11, 18 (Oahu: North Poamoho Stream). Holotype BPBM 10512; paratypes BPBM 122301; paratypes MCZ 138642 (fig. 9) and 138643 from Poamoho Gulch south of Pa Kanaka Plateau [and additional type lots from other localities].

roseoplica Pilsbry and Cooke, *Achatinella* (*Bulimella*) *sowerbyana*
1914, MofC (2) **22**: 180, pl. 34, fig. 12 (Oahu: Opaeula above forest–fence line). Lectotype ANSP 107990a (fig. 12) selected by Baker (1963: 196); paralectotypes MCZ 31150.

rotelloidea Mighels, *Helicina*
1845, PBSNH **2**: 19 (Oahu [Kauai]). Lectotype MCZ 156499 selected by Johnson (1949, OPM **1**: 228, pl. 27, fig. 21).

rotunda Gulick, *Achatinella*
1858, ALNHNY **6**: 249, pl. 8, fig. 67 (Oahu: Kaawa [Kaaawa] and Kahana). Holotype MCZ 39833 from Kaaawa; paratypes MCZ 170079 and 170083; *both* from Kahana.

rubella Pease, *Succinea*
1871, PZS for 1871: 460 (Lanai). Lectotype MCZ 161671 selected by Johnson (1994, BMCZ **154**: 22, pl. 4, fig. 13).

rubens Gould, *Achatinella*
1845, PBSNH **2**: 27 (Sandwich [Hawaiian] Islands); 1862, *Otia Conch.*, p. 195. Lectotype MCZ 169350 selected by Johnson (1964, USNM *Bull.* **239**: 142, pl. 42, fig. 6); paralectotypes MCZ 169351.

rubicunda Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 229, pl. 11, fig. 38, (Oahu: Konahuanui Mt.). Holotype ANSP 65719a, *teste* Baker (1963: 199).

rubida Gulick [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 84, pl. 10, fig. 12 (Oahu: Kahuku). Holotype MCZ 39888; paratypes MCZ 136727.

rubiginosa Gould, *Helix*
1846, PBSNH **2**: 173 (Kauai); 1852, USEE **12**: 50, pl. 4, figs. 49, 49a–c; 1862, *Otia Conch.*, pp. 21, 243. Holotype USNM 5449.

rubiginosa Newcomb, *Achatinella*
1854, PZS **21**: 154 (preprint p. 28), pl. 24, fig. 69 (Oahu: Palolo). Lectotype, here selected, BMNH 1992213/1 is the figured type, *teste* Welch; paralectotypes BMNH 1992213/2; CU 30103; MCZ 294961.

rubinia Hyatt [in] Hyatt and Pilsbry, *Amastra* (*Amastrella*) *rubens*
1911, MofC (2) **21**: 193, pl. 32, fig. 16 (Oahu: Kukuiala). Lectotype ANSP 92481a (fig. 16) selected by Baker (1963: 199); paralectotypes USNM 4710 and MCZ 136759 ex BSNH.

rubristoma Baldwin, *Amastra*
1906, *Nautilus* **19**: 137 (Lanai). Syntypes ANSP [no number] figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 242, pl. 39, figs. 5, 6); [holotype] ANSP 113063a [which type not indicated], *teste* Baker (1963: 199).

rufa Newcomb, *Achatinella*
1853, ALNHNY **6**: 21 (Molokai); 1854, PZS **21**: 130 (preprint p. 4), pl. 22, fig. 3. Lectotype, here selected, BMNH 1992203/1 is the measured and figured type; paralectotypes BMNH 1992203/2; CU 30105; MCZ 25820–25822 and 294938.

rugata Pease, *Helix*
1866, AJC **2**: 291 (Sandwich [Hawaiian] Islands); 1871, PZS for 1871: 474 as *Endodonta* (Maui). Lectotype MCZ 17237 selected by Johnson (1994, BMCZ **154**: 22, pl. 3, fig. 3); paralectotypes MCZ 298479; not located in ANSP by Baker (1963: 233), or elsewhere by Solem (1976: 377).

rugosa Newcomb, *Achatinella*
1854, PZS **21**: 138 (preprint p. 12), pl. 22, figs. 22, 22a (Oahu: Ewa). Lectotype, here selected, BMNH 1992212/1 is the figured type (fig. 22); figured paralectotype (fig. 22a) BMNH 1992212/2; paralectotypes BMNH 1992212/3; CU 30109; MCZ 25726 and 294968.

rugulosa Pease, *Amastra*
1870, JdeC **18**: 95 (Kauai); Crosse, 1876, JdeC **24**: 99, pl. 1, figs. 4, 4a. Holotype and fragment of paratype in MNHN, *teste* Fischer-Piette (1950: 149 [as second reference to *A. A. rugulosa* only]); paratypes MCZ 45255.

rustica Gulick [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 84, pl. 10, fig. 17 (East Maui: Kula). Holotype MCZ 39895; paratypes MCZ 136899.

rutila Newcomb, *Achatinella*

1854, PZS **21**: 135 (preprint p. 12), pl. 22, fig. 21 (Oahu: Niu). Lectotype, here selected, BMNH 1992211/1 is the figured type; paralectotypes BMNH 1992211/2; CU 30113; MCZ 25696.

sanguinea Newcomb, *Achatinella*
1854, PZS **21**: 138(preprint p. 9), pl. 22, fig. 15 (Oahu: Lehui). Lectotype, here selected, BMNH 1992242/1 is the measured and figured type; paralectotypes BMNH 1992242/2; CU 30114; MCZ 141213 and 294927.

saxatilis Gulick, *Achatinella*
1856, ALNHNY **6**: 187, pl. 6, fig. 15 (Oahu: Mokuleia). Holotype MCZ 39811; paratypes MCZ 45226 and 136925.

saxicola Baldwin, *Amastra*
1903, *Nautilus* **17**: 34 (Hawaii: [Kahuka Ranch], Kau). Syntype [no number] figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 317, pl. 47, fig. 16) not found in ANSP by Baker (1963); syntypes MCZ 135768, syntypes BPBM 23148.

scitula Gulick, *Achatinella*
1858, ALNHNY **6**: 241, pl. 8, fig. 61 (Oahu: Hakipu). Holotype only, MCZ 39850.

scutilus Mighels, *Bulimus*
1845, PBSNH **2**: 20 (Oahu). Not located by Johnson (1949: 228).

semicarinata Newcomb, *Achatinella*
1854, PZS **21**: 156 (preprint p. 30), pl. 24, fig. 76 (Ranai [Lanai]). Lectotype, here selected, BMNH 1992236/1 is the figured type; paralectotypes BMNH 1992236/2; CU 30116, but not located in CU by Clarke (1960: 154); not in MCZ.

seminuda Baldwin, *Amastra*
1906, *Nautilus* **19**: 137 (Molokai: Waikolu). Syntypes Baldwin collection figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 264, pl. 37, figs. 18–20); [holotype] ANSP 113054a [which type not indicated], *teste* Baker (1963: 199).

semiplicata Pease, *Melampus* (*Tralia*)
1860, PZS **28**: 146 (Sandwich [Hawaiian] Islands). Lectotype BMNH 1962773 selected by Kay (1965, *Bull.* BMNH, *Zool.* Suppl. 1: 30, pl. 4, fig. 7); paralectotypes MCZ 176566.

semivestita Hyatt and Pilsbry, *Laminella venusta*
1911, MofC (2) **21**: 349, pl. 51, figs. 6–10, 12 (Molokai). Lectotype ANSP 92686a (fig. 8) selected by Baker (1963: 199); paralectotypes MCZ 165673 ex BSNH.

senilis Baldwin, *Amastra*
1903, *Nautilus* **17**: 35 (Hawaii: Palihoukapapa on the Hamakua slope of Maunakea, at an elevation of 4,000 feet). Holotype ANSP 113076a figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 311, pl. 47, fig. 5) [broken], *teste* Baker (1963: 199).

sepulta Pilsbry and Cooke, *Amastra humilis*
1914, MofC (2) **23**: 39, pl. 7, figs. 15–17 (Molokai: Pleistocene of the sand dunes of Moomomi, around base of the bluff). Lectotype ANSP 110595a (fig. 15) selected by Baker (1963: 199); paralectotype MCZ 97641.

serrula Cooke [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 93, pl. 25, figs. 13, 14 (Oahu: Mt. Konahuanui at about 3,000 feet; Kuliouou). Holotype BPBM 42388; paratypes MCZ 141615 from Mt. Konahuanui.

setigera Gould, *Helix* [*Pitys*]
1844, PBSNH **1**: 174 (Sandwich [Hawaiian] Islands]), non Sowerby 1841; 1852, USEE **12**: 55, pl. 4, figs. 52, 52a–c (East Maui), as *Helix hystrix* Mighels which was listed there by Gould as having been described and figured by Pfeiffer (1846, *Symbolae ad Historiam Heliceorum* (Casselis) **3**: 67 and 1852 [in] Martini and Chemnitz, *Systematisches Conchylien-Cabinet* (2) **1**(pt. 12, sec. 2): 132, pl. 89, figs. 8–11); 1862, *Otia Conch.*, pp. 194, 243. Thus *Helix hystrix* "Mighels" Gould is a subjective synonym. In spite of the statement by Johnson (1961: 148), the figured holotype is USNM 5453; paratypes MCZ 169367 and 87861.

similaris Pease, *Amastra rugulosa*
1870, JdeC **18**: 96 (Kauai [Waimea]). Lectotype MCZ 45253 selected by Johnson (1994, BMCZ **154**: 24, pl. 2, fig. 11); paralectotypes MCZ 58936 and 298498.

simplex Pease, *Helicter* (*Leptachatina*)
1869, JdeC **17**: 170 (Hawaii). Measured holotype in MNHN, *teste* Fischer-Piette (1950: 73); paratype ANSP 57821 figured by Cooke (1910, MofC (2) **21**: 38, pl. 1, figs. 8, 9); paratypes MCZ 45176.

simulator Pilsbry and Cooke, *Achatinella cestus*
1914, MofC (2) **22**: 288, pl. 55, figs. 2–4 (Oahu: Palolo; Gulick). Holotype ANSP 92592a (fig. 2) *teste* Welch (1942: 34, pl. 4, fig. 12); paratypes MCZ 40219 ex Gulick collection.

singularis Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Limbatipupa*)
1920, MofC (2) **25**: 320, pl. 29, fig. 8 (Oahu: Kaliuwaa, on the rocky walls of the canyon, near the waterfall). Holotype BPBM 11077; paratypes MCZ 78810.

sinistrosa Baldwin, *Amastra* (*Laminella*)
1906, *Nautilus* **19**: 138 (Hawaii: Hamakua). Syntype Baldwin collection figured by Hyatt and Pilsbry (1911, MofC (2) **21**: 310, figs. 6, 7); [holotype] ANSP 113079a, *teste* Baker (1963: 199).

solida Pease, *Helicter* (*Amastra*)
1869, JdeC **17**: 173 (Oahu). Two of three syntypes from MCZ 23341 and 141338 figured by Pilsbry and Cooke (1914, MofC (2) **23**: 28, pl. 7, figs. 2, 3); syntype in MNHN *teste* Fischer-Piette (1950: 73).

solitaria Newcomb, *Achatinella*
1854, PZS **21**: 150 (preprint p. 24), pl. 24, fig. 60 (Oahu: Palolo). Holotype BMNH 1992225 is the only specimen, *teste* Newcomb. Five specimens under this name MCZ 241420, ex Gulick collection 614 from Niu, with the note "one of these received from Newcomb" [not marked].

sordida Newcomb, *Achatinella*
1854, PZS **21**: 139 (preprint p. 13), pl. 23, fig. 27 (Oahu: Lettui [Lihui]). Syntypes CU 30118 men-

tioned by Welch (1938: 31); syntypes MCZ 294942; not located in BMNH by Welch (1938:31) or by Naggs (personal communication).

soror Newcomb, *Achatinella*
1854, PZS **21**: 143 (preprint p. 17), pl. 23, figs. 36, 38 (Maui). Lectotype, here selected, BMNH 1992-253/1 (fig. 36); paralectotypes BMNH 1992253/2; CU 30119; MCZ 88128 and 294928.

spadicea Gulick, *Achatinella*
1858, ALNHNY **6**: 247, pl. 8, fig. 65 (Oahu: Kahana). Holotype only, MCZ 39840 refigured by Welch (1954, PANSP **106**: 87, pl. 1, fig. 14); specimen identified by Gulick [idiotype] from Hakipuu figured by Welch (*ibid.*, fig. 15).

spaldingi Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 248, pl. 21, figs. 10, 12, 13 (Oahu: Puu Kaua). Holotype BPBM 11048 (figs. 12, 13); paratypes MCZ 78761.

spaldingi Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 230, pl. 53, figs. 6–8 (Oahu: Kaaawa). Figured syntypes BPBM 36259; syntypes ANSP 111845 and MCZ 97517.

spaldingi Neal, *Pleuropoma laciniosa*
1934, BPBM *Bull.* **125**: 48, figs. 49, 50 (Oahu: Waianae Mountains, Puu Kaala, near spring; elevation about 3,000 feet). Holotype BPBM 11217; paratypes MCZ 191114.

sphaerica Pease, *Amastra*
1870, JdeC **18**: 94 (Kauai [Waimea]); Crosse, 1876, JdeC **24**: 98, pl. 1, figs. 5, 5a. Holotype and paratype in MNHN, *teste* Fischer-Piette (1950: 149 [as first reference to *A. A. rugulosa*]); paratypes MCZ 45162.

spinigera Cooke and Pilsbry [in] Pilsbry, *Pronesopupa* (*Pronesopupa*) *boettgeri*
1920, MofC (2) **26**: 10, pl. 1, fig. 11 (Oahu: Luakaha, Nuuanu). Holotype BPBM 11031; paratypes MCZ 78814.

splendida Newcomb, *Achatinella*
1853, ALNHNY **6**: 20 (Mani [Maui]: Waialuku); 1854, PZS **21**: 131 (preprint p. 5), pl. 22, fig. 4. Lectotype, here selected, BMNH 1992205/1 is the figured type, so marked; paralectotypes BMNH 1992205/2; CU 30122; MCZ 294925.

stellula Gould, *Helix* [*Pityn*]
1844, PBSNH **1**: 174 (Sandwich [Hawaiian] Islands); 1852, USEE **12**: 56, pl. 4, figs. 52+, 52a+–c+ (Maui). Lectotype MCZ 169383 selected by Johnson (1964, USNM *Bull.* **239**: 152, pl. 38, fig. 3).

stiria Gulick, *Achatinella*
1856, ALNHNY **6**: 194, pl. 6, fig. 22 (Oahu: Helemanu [Helemano], Peula, and Kawailoa). Holotype only, MCZ 239808 from Helemano.

straminea Cooke [in] Pilsbry and Cooke, *Auriculella*
1915, MofC (2) **23**: 77, pl. 24, fig. 13 (Oahu: Mt. Tantalus). Holotype BPBM 42366; paratype MCZ 73033.

striata Newcomb, *Tornatellina*
1861, PCANS **2**: 93 (Kauai). Not located in CU by Clarke (1960: 154); Cooke (1910: 62) suggested that "[p]robably the type was in the California Academy and is now destroyed [in the 1909 earthquake] . . . ." However, all of the other taxa described in the same paper are represented by type material in CU.

striatella Gulick, *Achatinella*
1856, ALNHNY **6**: 178, pl. 6, fig. 6 (Oahu: on the mountain ridge of Keawaawa). Holotype MCZ 39805; paratypes MCZ 40300 and 136987.

striatula Gould, *Achatinella* [*Leptachatina*]
1845, PBSNH **2**: 28 (Sandwich [Hawaiian] Islands); 1862, *Otia Conch.*, p. 196, ". . . is *A. clara* Pfeiffer (1860)." Syntypes MCZ 169386, "The bottle in which are the types of this species, contains a varied assortment of different species" (Cooke, 1911: 75).

striatula Pease, *Vertigo*
1871, PZS for 1871: 461 (Hawaii: [Kalapana, Puna]). Lectotype MCZ 45239 selected by Johnson (1994, BMCZ **154**: 25), is the syntype figured by Pilsbry and Cooke (1926, MofC (2) **27**: 223, pl. 28, figs. 1, 2); paralectotypes MCZ 151647 and BPBM ex MCZ.

subassimilis Hyatt [in] Hyatt and Pilsbry, *Amastra assimilis*
1911, MofC (2) **21**: 307, pl. 46, figs. 7, 8 (Maui: Waialua). Figured holotype MCZ 136876; paratypes MCZ 136877; *both* ex Gulick collection 1519.

subcentralis Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Infranesopupa*)
1920, MofC (2) **25**: 294, pl. 28, fig. 8 (Hawaii: Palihoukapapa). Holotype BPBM 18699; paratypes MCZ 78799.

subcornea Hyatt and Pilsbry, *Amastra* (*Metamastra*)
1911, MofC (2) **21**: 189, pl. 31, fig. 11 (Oahu: near the base of Round Top, toward Rocky Hill, where the Manoa road enters the valley back of Punahou; fossil). Holotype BPBM 23497; paratypes ANSP 104689 and MCZ 154740 ex BSNH 13397.

subcrassilabris Hyatt and Pilsbry, *Amastra* (*Amastra*)
1911, MofC (2) **21**: 293, pl. 45, figs. 14, 15 (East Maui: Kula; Gulick). Holotype MCZ 136902; paratype MCZ 136901; *both* ex Gulick collection 1541.

subobscura Hyatt and Pilsbry, *Amastra* (*Amastra*)
1911, MofC (2) **21**: 276, pl. 42, fig. 6 (Molokai: Ualapue). Holotype MCZ 154729 ex BSNH 13447.

subovata Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 37, pl. 11, fig. 2 (Lanai: [Koele Gulch]; Thaanum). Holotype BPBM 12063; paratypes MCZ 97693 and 202585.

subpolita Hyatt and Pilsbry [in] Pilsbry and Cooke, *Partulina* (*Partulina*)
1914, MofC (2) 22: 359, pl. 23, fig. 1 (Molokai: Ualapue). Figured holotype ANSP 106992, *teste* Baker (1963: 196); paratypes MCZ 190629.

subpolita Pilsbry and Cooke, [*Partulina*]

1912, MofC (2) **22**: 24 (Molokai). Published in a key to the Achatinellae of Molokai. Subsequently formally described by Hyatt and Pilsbry. See next reference.

subpulla Hyatt and Pilsbry, *Amastra* (*Amastra*) *affinis*
1911, MofC (2) **21**: 300, pl. 45, figs. 3, 4 (East Maui: Kula). Figured holotype MCZ 136897 (fig. 3); figured paratype MCZ 302521 (fig. 4); *both* ex Gulick collection 1546.

subrutila Mighels, *Helix*
1845, PBSNH **2**: 19 (Oahu). BPBM 36606 figured by Baker (1940, BPBM *Bull.* **165**: 163, pl. 41, fig. 2; pl. 28, fig. 15) appears to have been selected as neotype. Not located by Johnson (1964: 229).

subsoror Hyatt and Pilsbry, *Amastra* (*Heteramastra*)
1911, MofC (2) **21**: 287, pl. 48, figs. 6, 7 (West Maui: Lahaina). Figured holotype ANSP 57786a (fig. 6) *teste* Baker (1963: 199); paratypes MCZ 136893 ex Gulick collection and MCZ 154725 ex BSNH.

subtilissima Gould, *Helix* [*Zonites*]
1846, PBSNH **2**: 177 (Maui); 1852, USEE **12**: 48, pl. 5, figs. 62, 62a–c; 1862, *Otia Conch.*, p. 24. Lectotype USNM 5464 selected by Baker (1941: 216). Gould appears to have had before him only the single imperfect specimen figured. Specimens subsequently identified by Gould [idiotypes] MCZ 169384 and 169385.

subula Gulick, *Achatinella*
1856, ALNHNY **6**: 191, pl. 6, fig. 19 (Oahu: Palolo Valley). Holotype MCZ 39804; paratypes MCZ 45630.

subvirens Newcomb, *Achatinella*
1854, PZS **21**: 136 (preprint p. 10), pl. 22, fig. 18 (Oahu: Niu). Lectotype, here selected, BMNH 1992209/1 is the measured and figured type; paralectotypes BMNH 1992209/2; CU 30130; MCZ 25692 and 294931.

succincta Newcomb, *Achatinella*
1855, PBSNH **5**: 220 (Oahu: Ewa); 1866, AJC **2**: 213, pl. 13, fig. 7. Lectotype, here selected, CU 30132A is the figured type, so marked; paralectotypes CU 30132; MCZ 142990, 143004, and 294972; not in ANSP (Baker, 1963).

sulculosa Ancey, *Helicina*
1904, PMSL **6**: 127, pl. 7, fig. 25 (Hawaii: Olaa). Syntypes MCZ 191112.

swiftii Newcomb, *Achatinella*
1854, PZS **21**: 133 (preprint p. 7), pl. 22, figs. 9, 9a ([Oahu]: District of Ewa). Lectotype, here selected, BMNH 1992214/1 is the figured type (fig. 9); measured and figured (fig. 9a) paralectotype BMNH 1992214/2 is identified as *A. turgida* Newcomb by Pilsbry (1914: 308); paralectotypes BMNH 1992214/3; CU 30134; MCZ 25549 and 294978.

sykesi Pilsbry [in] Hyatt and Pilsbry, *Amastra* (*Amastra*)
1911, MofC (2) **21**: 273, pl. 42, figs. 2, 3 (Molokai: Halawa; Thaanum). Figured syntypes BPBM 5316 ex Thaanum; syntypes MCZ 31179 ex Thaanum and 97646 ex BPBM.

sykesii Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellaria*
1916, MofC (2) **23**: 265, pl. 55, fig. 6 (Hawaii: Hilo, Thaanum; Olaa, Thaanum, and Cooke). Holotype BPBM 14194 from Olaa, *teste* Cowie et al. (1995a: 82); paratypes ANSP 111858; paratypes MCZ 97565 and 141621 *both* from Olaa.

talpina Gulick, *Achatinella*
1856, ALNHNY **6**: 212, pl. 7, fig. 38 (Maui: Wailuku). Holotype MCZ 39863; paratypes MCZ 136568, 136572, and 136573.

tappaniana C. B. Adams, *Achatinella*
1851, *Contributions to Conchology* (8): 126 ([Maui]). Holotype MCZ 155949 figured by Johnson and Boss (1972, OPM **3**: 215, pl. 42, fig. 8).

tenebrosa Cooke, *Carelia*
1931, BPBM *Bull.* **85**: 75, pl. 14, figs. 6–8 (Kauai: on the upper slopes and top of Haupu, the highest peak of the Kipu range, 1,500–2,200 feet elevation). Holotype BPBM 86151a (fig. 7); paratypes MCZ 143813.

tenebrosa Pease, *Leptachatina*
1870, JdeC **18**: 92 (Kauai [Waimea]); Crosse, 1876, JdeC **24**: 97, pl. 3, fig. 5. Holotype in MNHN, *teste* Fischer-Piette (1950: 149); paratypes MCZ 45189 and 50110.

tenella Gould, *Vitrina*
1846, PBSNH **2**: 181 (Kauai); 1852, USEE **12**: 11, pl. 1, figs. 10, 10a–c; 1862, *Otia Conch.*, p. 26. Holotype USNM 20874.

tenerrima Ancey, *Succinea*
1904, PMSL **6**: 118, pl. 7, fig. 2 (Hawaii: Kaiwiki, 2,500–2,600 feet above sea level). Holotype BPBM 18995; paratypes BPBM 19037 and MCZ 31219.

tenuicostata Pease, *Helicter* (*Leptachatina*)
1869, JdeC **17**: 170 (Hawaii). Holotype in MNHN figured by Fischer-Piette (1950, JdeC **90**: 72, pl. 3, fig. 51).

tenuilabris Gulick [in] Gulick and Smith, *Amastra*
1873, PZS for 1873: 83, pl. 10, fig. 16 (Oahu: Pauoa). Holotype only, MCZ 39919.

tenuis Smith [in] Gulick and Smith, *Auriculella*
1873, PZS for 1873: 87, pl. 10, fig. 27 (Oahu: Kalaikoa, Wahiawa, Helemano, and Kawailoa). Lectotype, here selected, BMNH 1992201 is the figured and only type, from Helemano; paralectotypes MCZ 39917, from Kalaikoa.

tenuispira Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 232, pl. 11, fig. 51 (Oahu: Kaala Mt.). Figured holotype ANSP 65720a, *teste* Baker (1963: 199).

terebra Ancey, *Tornatellina*
1903 [1904], JdeC **51**: 303, pl. 12, figs. 17, 18 (Mani [Maui]: Kaupakalua). Not mentioned by Fischer-Piette (1950: 171); "type" BPBM 18450, *teste* Pilsbry and Cooke (1915: 245); paratypes MCZ 165797 and 199564.

terebra Newcomb, *Achatinella*

1854, PZS **21**: 144 (preprint p. 18), pl. 23, fig. 40 (West Maui). Lectotype, here selected, BMNH 1992216/1 is the figured type; paralectotypes BMNH 1992216/2; CU 30144; MCZ 294955.

terebralis Gulick, *Achatinella*
1856, ALNHNY **6**: 193, pl. 6, fig. 21 (Oahu: Kawailoa). Holotype MCZ 39806; paratypes MCZ 45234.

tessellata Newcomb, *Achatinella*
1853, ALNHNY **6**: 19 (Molokai); 1854, PZS **21**: 139 (preprint p. 13), pl. 23, fig. 26 (Molokai: Kalai). Lectotype, here selected, BMNH 1992213/1 is the figured type; paralectotypes BMNH 1992213/2; CU 30147; MCZ 25816, 186537, and 294956.

tetrao Newcomb, *Achatinella*
1855, PZS **22**: 311; 1855, PBSNH **5**: 219 (Ranai [Lanai]); 1866, AJC **2**: 214, pl. 13, figs. 11, 12. Lectotype, here selected, CU 30149A is the figured type, so marked; paralectotypes CU 30149; MCZ 141211; not found in ANSP by Baker (1963).

[*thaanumi*] *thaamuni* Pilsbry and Cooke, *Achatinella* (*Achatinellastrum*)
1914, MofC (2) **22**: 273, pl. 42, figs. 5, 6 (Oahu: Waianae range, a gulch of Mt. Kaala running into Haleauau; Thaanum). Holotype MCZ 190915 ex Thaanum. "We here select *thaanumi* as the correct original spelling." (Cowie et al., 1995a: 54).

thaanumi Ancey, *Succinea*
1899, PMSL **3**: 272, pl. 12, fig. 3 (Hawaii: Olaa). Syntypes [labeled paratypes] BPBM 19038; syntypes MCZ 190647.

thaanumi Cooke, *Carelia paradoxa*
1931, BPBM *Bull.* **85**: 92, pl. 16, fig. 8 (Kauai: south side of the [Wailua] River in a cane field south of gate, near the base of the Kalepa range). Holotype BPBM 49265; paratypes MCZ 202829.

thaanumi Cooke, *Leptachatina* (*Thaanumia*)
1911, MofC (2) **21**: 88, pl. 6, figs. 16, 17 (Molokai: Mapulehu ridge; Thaanum). Figured holotype BPBM 12023; paratypes MCZ 202829 ex Thaanum.

thaanumi Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 242, pl. 20, figs. 12, 13 (East Maui: Auwahi). Holotype BPBM 11043 (fig. 12); paratypes MCZ 78749.

thaanumi Pilsbry [in] Hyatt and Pilsbry, *Pterodiscus*
1911, MofC (2) **21**: 125, pl. 24, figs. 1, 2 (Oahu: Kukaeiole, near Kaaawa, on the northeastern coast). Figured holotype ANSP 95045a, *teste* Baker (1963: 199); paratypes MCZ 190557.

thaanumiana Pilsbry [in] Pilsbry and Cooke, *Partulina* (*Baldwinia*)
1913, MofC (2) **22**: 112, pl. 18, figs. 6, 7 (West Maui: Waiehu Gulch). Lectotype ANSP 110090 (fig. 6) selected by Baker (1963: 196); paralectotypes MCZ 190914.

thaumasia Cooke and Pilsbry [in] Pilsbry and Cooke, *Lyropupa*
1920, MofC (2) **25**: 270, pl. 24, figs. 13–15; pl. 25, fig. 14 (Kauai: Hanakapiai). Holotype BPBM 11061 (pl. 24, figs. 13–15); paratypes MCZ 78775.

theodorei Baldwin, *Achatinella* (*Partulina*)
1895, PANSP **47**: 226, pl. 10, fig. 27 (Molokai: Kawela). Figured holotype ANSP 65710a, *teste* Baker (1963: 196); paratype MCZ 104712.

thwingi Pilsbry and Cooke, *Partulina* (*Perdicella*)
1914, MofC (2) **22**: 357, pl. 54, figs. 6, 6a, 6b (East Maui: Auwahi; Thaanum). Lectotype ANSP 111441a (fig. 6) selected by Baker (1963: 196); paralectotypes MCZ 190598 and 190599 *both* ex Thaanum.

tiara Mighels, *Helix*
1845, PBSNH **2**: 19 (Kauai). Lectotype MCZ 176994 selected by Johnson (1949, OPM **1**: 229, pl. 27, fig. 23).

torrida Gulick, *Achatinella*
1858, ALNHNY **6**: 250, pl. 8, fig. 68 (Oahu: Kahana, Kaawa [Kaaawa], Waikane, and Waiolu). Holotype MCZ 39856; paratypes MCZ 39769–39771; *all* from Waiolu.

tricolor Smith [in] Gulick and Smith, *Achatinella*
1873, PZS for 1873: 76, pl. 9, fig. 6 (Oahu: Ioleka, in Heia). Holotype only, MCZ 39877.

trilineata Gulick, *Achatinella*
1856, ALNHNY **6**: 226, pl. 7, fig. 46 (Oahu: Palolo, Waialae, Wailupe, and Niu). Holotype MCZ 39882 from Waialae; paratypes MCZ 155639 from Palolo.

triplicata Pease, *Auriculella*
1868, JdeC **16**: 346 ([Oahu]). Lectotype MCZ 45150 selected by Johnson (1994, BMCZ **154**: 26, pl. 2, fig. 9); paralectotypes MCZ 298487; not located in MNHN by Fischer-Piette (1950: 71).

triticea Gulick, *Achatinella*
1856, ALNHNY **6**: 184, pl. 6, fig. 12 (Oahu: Keawaawa). Holotype MCZ 39807; paratypes MCZ 45235 and 147018.

tryphera Cooke and Pilsbry [in] Pilsbry and Cooke], *Nesopupa* (*Nesodagys*) *wesleyana*
1920, MofC (2) **25**: 301, pl. 29, fig. 3 (Oahu: Palolo). Holotype BPBM 11082; paratypes MCZ 78792.

tsunami Cooke and Kondo, *Carelia pilsbryi*
1952, BPBM *Occ. Pap.* **20**(20): 335, figs. 3a–d (Kauai: Lepeuli Beach). Figured syntypes BPBM 190567A–D; syntypes MCZ 187596.

tuberans Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 81, pl. 10, fig. 3 (Oahu: metropolis of the species is Kalaikoa; it is also found in Ahonui; and single specimens have been brought up from Wahiawa and Helemano). Holotype only, MCZ 39900 from Kalaikoa.

tumefactus Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 82, pl. 9, fig. 20 ([Oahu]: Wahiawa, rarely in Helemano). Holotype only, MCZ 39908 from Wahiawa.

turbiniformis Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 81, pl. 10, fig 7 (Oahu: Kalaikoa and Lehui). Holotype only, MCZ 39910 from Lehui.

turgida Newcomb, *Achatinella*

1854, PZS **21**: 134 (preprint p. 8), pl. 22, figs. 10, 10a (Oahu: Ewa). Lectotype BMNH 1992192/1 (fig. 10) selected and refigured by Welch (1942, SMC *103*(1): 68, pl. 6, fig. 2 [fig. 3 on plate caption]); figured (fig. 10a) paralectotype BMNH 1992192/2; paralectotypes BMNH 1992192/3; CU 30154; MCZ 25540 and 294936.

turgidula Pease, *Leptachatina*
1870, JdeC **18**: 89 (Kauai: [Waimea]); Crosse, 1876, JdeC **24**: 96, pl. 4, fig. 5. Holotype in MNHN, *teste* Fischer-Piette (1950: 149); paratypes MCZ 45182 and 45183.

turgidula Pease, *Limnaea*
1870, AJC **6**: 5, pl. 3, fig. 3 (Oahu). Lectotype MCZ 298901 selected by Johnson (1994, BMCZ **154**: 26, pl. 4, fig. 11); paralectotypes MCZ 298902; two paralectotypes ANSP 21923, though not located in ANSP by Baker (1964: 154).

turricula Mighels, *Achatina*
1845, PBSNH **2**: 20 (Oahu [Kauai, Waioli-Waipa Ridge, *teste* Cooke (1931: 61)]). Lectotype MCZ 156495 selected by Johnson (1949, OPM **1**: 230, pl. 27, fig. 8); paralectotypes MCZ 156042.

turrita Gulick, *Achatinella*
1856, ALNHNY **6**: 192, pl. 6, fig. 20 (Oahu: Lihue). Holotype MCZ 39825; paratypes MCZ 136917.

ualapuensis Pilsbry and Cooke, *Newcombia cinnamomea*
1912, MofC (2) **22**: 12, pl. 2, figs. 11, 12 (Molokai: Ualapue, Kahaanui). Figured holotype ANSP 94490a, *teste* Baker (1963: 196); paratypes MCZ 190547 from Ualapue.

uberta Gould, *Helicina*
1847, PBSNH **2**: 202 (Maui and Oahu Mountains); 1852, USEE **12**: 94, pl. 7, figs. 114, 114a–c. Holotype USNM 5516; paratypes MCZ 169411, 186722, and 216585; localities not differentiated.

ultima Pilsbry and Cooke, *Amastra* (*Cyclamastra*)
1914, MofC (2) **23**: 25, pl. 2, figs. 9, 10 (Hawaii: Kahuku, Kau). Lectotype ANSP 108146a (fig. 10) selected by Baker (1963: 199); paralectotype MCZ 97599.

umbilicata Ancey, *Auriculella*
1889, BMSF **6**: 232 (Maui: Lahaina). Holotype BPBM 18451, *teste* Pilsbry and Cooke (1916: 260); paratypes MCZ 165798.

umbilicata Mighels, *Physa*
1845, PBSNH **2**: 21 (Oahu). Not located by Johnson (1949: 230).

umbrosa Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 229, pl. 11, figs. 36, 37 (Molokai: Kamalo). Figured syntypes ANSP 65714; [holotype] ANSP 65714a [which type not indicated], *teste* Baker (1963: 199).

undata Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 230, pl. 11, fig. 39 (Oahu: Nuuanu). Figured holotype ANSP 65722, *teste* Baker (1963: 199).

undosa Gulick, *Achatinella*
1856, ALNHNY **6**: 205, pl. 7, fig. 33 (Maui: Waihee). Holotype MCZ 39848; paratypes MCZ 136525.

undulata Newcomb, *Achatinella*
1855, PBSNH **5**: 218 (Oahu: Waialua); 1866, AJC **2**: 216, pl. 13, fig. 15. Lectotype, here selected, CU 30160A is the figured type, so marked; paralectotypes CU 30160 and MCZ 294966; not located in ANSP by Baker (1963).

uniplicata Pease, *Auriculella*
1868, JdeC **16**: 344, pl. 14, figs. 7, 7a (Maui: [Lahaina]). Two figured syntypes in MNHN, *teste* Fischer-Piette (1950: 71); syntypes MCZ 159563 and 161636.

ustulata Gulick, *Achatinella*
1856, ALNHNY **6**: 211, pl. 7, fig. 37 (Maui: Beautiful Valley). Holotype only, MCZ 39853.

varia Cooke, *Leptachatina* (*Leptachatina*)
1910, MofC (2) **21**: 32, pl. 11, fig. 1 (Molokai: Paliko-1 in Halawa and fossil at the mouth of Halawa Valley; Thaanum). Holotype BPBM 12066; paratypes MCZ 97685 ex Cooke and 202554 ex Thaanum.

varia Gulick, *Achatinella*
1856, ALNHNY **6**: 222, pl. 7, fig. 43 (Oahu: Palolo, Waialae and Wailupe). Holotype MCZ 39843 from Palolo; paratypes MCZ 159620 and 159629; *both* from Waialae.

variabilis Newcomb, *Achatinella*
1854, PZS **21**: 154 (preprint p. 28), pl. 24, fig. 70 (Ranai [Lanai]). Lectotype, here selected, BMNH 1992232/1 is the figured type; paralectotypes BMNH 1992232/2; CU 30164; MCZ 25856 and 294979.

variabilis Pease, *Carelia*
1871, JdeC **18**: 402 (Kauai). Single specimen found; not mentioned by Fischer-Piette (1950: 76), or found by Johnson (1994).

venulata Newcomb, *Achatinella*
1854, PZS **21**: 146 (preprint p. 20), pl. 23, figs. 48, 48a (Oahu: Kolau). Is *A. producta* Reeve, *teste* Newcomb (1858: 315). Lectotype, here selected, BMNH 1992220/1 (fig. 48); paralectotype BMNH 1992220/2; not located in CU by Clarke (1960: 155); not in MCZ.

venusta Gould, *Succinea*
1846, PBSNH **2**: 186 (Hawaii); 1852, USEE **12**: 22, pl. 2, figs. 25, 25a–c (Hawaii: Mount [Mauna] Kea at an elevation of 7,000 feet); 1862, *Otia Conch.*, p. 30. Figured holotype USNM 5425; paratypes MCZ 39647 and 169417.

venusta Mighels, *Achatinella*
1845, PBSNH **2**: 21 (Oahu [Molokai]). Neotype Portland Society of Natural History 218, selected by Hyatt and Pilsbry (1911, MofC (2) **21**: 348, pl. 51, fig. 12). Most of the Portland collection went to the MCZ in 1962, the rest to the Delaware Museum of Natural History. The neotype has not been located at either institution. The type figured by Reeve (1850, *Conchologia Iconica 6 Achatinella*, pl. 5, species 32) not located in BMNH by Naggs (per-

sonal communication); not located by Johnson (1949: 230).

versicolor Gulick [in] Gulick and Smith, *Apex*
1873, PZS for 1873: 80, pl. 9, fig. 18 (Oahu: Ahonui and Kalaikoa). Holotype MCZ 39907; paratypes MCZ 147191, 147192, and 147197; *all* from Ahonui; paratypes MCZ 147193, 147194, and 147196; *all* from Kalaikoa.

versipellis Gulick, *Achatinella*
1856, ALNHNY **6**: 224, pl. 7, figs. 44a, b (Oahu: Pohakunui, in Kailua). Holotype MCZ 39837 (fig. 44a); paratype MCZ 39871 (fig. 44b is variety b).

vesicalis Gould, *Succinea*
1846, PBSNH **2**: 183 (Hawaii: Mauna Kea, elevation of 7,000 ft.); 1852, USEE **12**: 21, pl. 2, figs. 17, 17a; 1862, *Otia Conch.*, pp. 28, 244. Holotype USNM 5417, reduced to fragments.

vespertina Baldwin, *Achatinella* (*Apex*)
1895, PANSP **47**: 219, pl. 10, fig. 14 (Oahu: Kawailoa). Figured holotype ANSP 65699a, *teste* Baker (1963: 197).

vestita Mighels, *Achatinella*
1845, PBSNH **2**: 20 ([Oahu]: Waianai [Waianae]; Hawaii). Syntypes Jay collection [no number]. Listed by Jay (1850: 215) as a synonym of *Achatinella decora* Férussac. Not located by Johnson (1949: 230).

vetuscula Cooke, *Amastra* (*Amastra*) *uniplicata*
1917, BPBM *Occ. Pap.* **3**(3): 244, pl. A, fig. 5 (Molokai: Pleistocene of the shifting sands north of Mauna Loa and directly south of Laina where the pipe line crosses the shifting sands). Holotype and paratypes [listed as cotypes] BPBM 41992; paratypes MCZ 97645.

vetusta Baldwin, *Amastra* (*Amastra*)
1895, PANSP **47**: 233, pl. 11, fig. 50 (Oahu: near the base of Punchbowl Hill . . . . Twenty or thirty feet above sea level, near Honolulu). Figured holotype ANSP 65717a, *teste* Baker (1963: 199).

violacea Newcomb, *Achatinella*
1853, ALNHNY **6**: 18 (Molokai); 1854, PZS **21**: 135 (preprint p. 9), pl. 22, fig. 14. Lectotype, here selected, BMNH 1992241/1 is the figured type; paralectotypes BMNH 1992241/2, CU 30174; MCZ 141459 and 156035.

virens Gulick, *Achatinella*
1858, ALNHNY **6**: 254, pl. 8, fig. 73 (Oahu: Halawa and Nuuanu). Holotype only, MCZ 39880 from Nuuanu.

virgula Cooke and Pilsbry [in] Pilsbry and Cooke, *Tornatellides*
1915, MofC (2) **23**: 241, pl. 51, figs. 10, 14 (East Maui: Kaupakalua). Figured syntypes BPBM 36264; syntypes ANSP 111849 and MCZ 97543.

virgulata Mighels, *Partula*
1845, PBSNH **2**: 20 ([Oahu]: Waianai [Waianae] [is from Molokai, *teste* Pilsbry and Cooke (1912: 26)]). Lectotype MCZ 177008 selected by Johnson (1949, OPM **1**: 231, pl. 37, fig. 9); paralectotypes MCZ 156037.

viridans Mighels, *Achatinella*
1845, PBSNH **2**: 20 (Oahu). Lectotype MCZ 188052 selected by Johnson (1954, OPM **1**: 447, pl. 58, fig. 1).

viridis Pease, *Carelia variabilis*
1870, JdeC **18**: 402 (Kauai: east side). Pilsbry and Cooke (1914, MofC (2) **23**: 16, pl. 9, fig. 11) suggest that this specimen figured from MCZ 23343 may be the type of *viridis*; not mentioned by Fischer-Piette (1950: 76).

vitrea Newcomb, *Achatinella*
1854, PZS **21**: 142 (preprint p. 16), pl. 23, fig. 34 (Oahu: near the summit of the mountain ridge dividing Manoa from Palolo Valley). Lectotype, here selected, BMNH 1992251/1 is the figured type; paralectotypes BMNH 1992251/2; CU 30181; MCZ 142991 and 294965.

vitreola Gulick, *Achatinella*
1856, ALNHNY **6**: 194, pl. 6, fig. 23 ([West Maui]). Holotype MCZ 39809; paratype MCZ 45236.

vittata Reeve, *Achatinella*
1850, *Conchologia Iconica 6, Achatinella*, pl. 2, species 9 ([Oahu]). Lectotype, here selected, BMNH 1996009/1, is the figured type; paralectotypes BMNH 1996009/2; paralectotypes MCZ 25523 ex Cuming.

volutata Gould, *Limnea*
1847, PBSNH **2**: 211 (Oahu); 1852, USEE **12**: 122, pl. 9, figs. 142, 142a, b. Probable holotype USNM 5542; paratypes MCZ 169427 and 216788.

waianaensis Cooke and Pilsbry [in] Pilsbry and Cooke, *Nesopupa* (*Nesopupilla*)
1920, MofC (2) **25**: 281, pl. 27, figs. 4–6 (Oahu: Waianae Mts. at Pukaloa, in the open valley near the "Hunter's Cabin"). Holotype BPBM 11064; paratypes MCZ 78782.

waianaensis Pilsbry and Cooke, *Laminella gravida*
1915, MofC (2) **23**: 54, pl. 1, figs. 7, 8 (Oahu: Haleauau, Waianae Mountains). Holotype ANSP 109903a (fig. 8) *teste* Baker (1963: 199); paratypes MCZ 31204.

wailauensis Pilsbry and Cooke, *Newcombia canaliculata*
1912, MofC (2) **22**: 7, pl. 14, fig. 5 (Molokai: Wailau). Lectotype ANSP 110069a (fig. 5) selected by Baker (1963: 197); paralectotypes MCZ 19053 and 31211.

wailauensis Pilsbry [in] Hyatt and Pilsbry, *Amastra* (*Amastra*) *violacea*
1911, MofC (2) **21**: 258, pl. 39, figs. 13, 14; pl. 27, figs. 1, 2 (Molokai: Wailau). Figured holotype ANSP 104670 (pl. 39, fig. 14) *teste* Baker (1963: 199); paratype MCZ 97608.

wesleyana Ancey, *Nesopupa*
1904, PMSL **6**: 123, pl. 7, fig. 16 (Hawaii: Hilo [and other localities]). Holotype BPBM 18704, *teste* Cooke and Pilsbry (1920: 300); paratypes MCZ 78791 and 199569.

wheatleyana Pilsbry [in] Pilsbry and Cooke, *Achatinella* (*Bulimella*) *elegans*
1913, MofC (2) **22**: 168, pl. 28, figs. 11, 11a, b

(Oahu: Punaluu; Gulick). Holotype ANSP 92449 (fig. 11a); paratypes MCZ 170034 ex Gulick.

winniei Baldwin, *Partulina*
1908, *Nautilus* **22**: 67 (West Maui: Kahakuloa). Syntypes ANSP [no number] figured by Pilsbry and Cooke (1912, MofC (2) **22**: 44, pl. 13, figs. 1–3). [Holotype] ANSP 10508a [which type not indicated], *teste* Baker (1963: 197).

zebra Newcomb, *Achatinella*
1855, ALNHNY **6**: 142 (East Maui). Specimens identified by Newcomb [idiotypes] CU 30185, *teste* Clark (1960: 156); not in MCZ.

zonata Gulick, *Achatinella*
1858, ALNHNY **6**: 238, pl. 8, fig. 58 (Oahu: Waimea, Pupukea, Waialei, Kahuku, Hauula, and Kaawa [Kaaawa]). Holotype only, MCZ 39851 from Waialei.

LIST OF SPECIES BY AUTHOR

Adams, Charles Baker

decepta, Achatinella
dimondi, Achatinella
dubiosa, Achatinella tappaniana
lata, Achatinella dimondi
magna, Achatinella
modesta, Achatinella
reevei, Achatinella
tappaniana, Achatinella

Ancey, César-Marie Félix

abbreviata, Tornatellina
baldwini, Helicina
baldwini, Nesopupa
carbonaria, Lyropupa
casta, Succinea
cincta, Tornatellina
clathratula, Lyropupa
cyphostyla, Tornatellina
delicata, Succinea
dissotropis, Helicina
euryomphala, Tornatellina
extincta, Tornatellina
garrettiana, Succinea
hawaiiensis, Lyropupa mirabilis
heliciformis, Amastra
henshawi, Tornatellina
macromphala, Tornatellina
macroptychia, Tornatellides
malleata, Auriculella
microthauma, Lyropupa
phaeostoma, Partulina physa
plicifera, Nesopupa
prisca, Lyropupa magdalenae
procerula, Tornatellina
quadrata, Succinea
sulculosa, Helicina
tenerrima, Succinea
terebra, Tornatellina
thaanumi, Succinea
umbilicata, Auriculella
wesleyana, Nesopupa

Baldwin, Dwight David

anceyana, Achatinella
antigua, Amastra
aspera, Laminella
aurostoma, Amastra
badia, Amastra
breviata, Amastra
canaliculata, Achatinella
carinella, Newcombia
carnicolor, Partulina
conica, Amastra
cookei, Achatinella
cooperi, Partulina
cyclostoma, Amastra
depicta, Laminella
dolei, Achatinella
duoplicata, Laminella
ernestina, Achatinella
flemingi, Partulina
fossilis, Amastra
fulvicans, Partulina
hawaiiensis, Achatinella
hayseldeni, Partulina
helvina, Laminella
henshawi, Amastra
horneri, Achatinella
juddii, Achatinella
kaaeana, Partulina
knudsenii, Amastra
lemmoni, Partulina
luteostoma, Achatinella
lymaniana, Achatinella
lyonsiana, Achatinella
montana, Amastra
mucida, Achatinella
multizonata, Achatinella
mutabilis, Partulina
nana, Amastra
nivea, Achatinella
pellucida, Amastra
pullata, Amastra
rubicunda, Amastra
rubristoma, Amastra
saxicola, Amastra
seminuda, Amastra
senilis, Amastra
sinistrosa, Amastra
tenuispira, Amastra
theodorei, Achatinella
umbrosa, Amastra
undata, Amastra
vespertina, Achatinella
vetusta, Amastra
winniei, Partulina

Cockerell, Theodore Dru Alison

cookei, Endodonta

Cooke, Charles Montague, Jr.

acuminata, Amastra subrostrata
alexandri, Gulickia
anceyana, Leptachatina
annosa, Amastra rugulosa
attenuata, Leptachatina
baldwiniana, Lyropupa rhabdota
brevis, Leptachatina pachystoma
capitosa, Leptachatina
concolor, Leptachatina
cylindrella, Leptachatina pachystoma
delicata, Amastra
dulcis, Leptachatina
emortua, Amastra flavescens
fastigata, Amastra rugulosa
flavida, Auriculella
fragosa, Amastra
fulgida, Leptachatina
gentilis, Amastra conica
glossema, Carelia
haena, Laxisuccinea
haupuensis, Godwinia
illimis, Leptachatina
inopinata, Amastra
isenbergi, Carelia dolei
kalalauensis, Carelia
knudsenii, Leptachatina
kulnsi, Amastra
laevigata, Leptachatina
lanaiensis, Auriculella
lanaiensis, Leptachatina
lanaiensis, Lyropupa rhabdota
lepida, Leptachatina
longiuscula, Leptachatina
meineckei, Amastra anthonii
micra, Leptachatina brevicula
molokaiensis, Leptachatina
montana, Auriculella
morbida, Leptachatina
nannodes, Amastra
occidentalis, Leptachatina nitida
olivacea, Auriculella
ovatula, Amastra
pagodula, Amastra
paulula, Amastra
perversa, Auriculella
pilsbryi, Leptachatina
pilsbryi, Tornatellides
pluscula, Amastra umbilicata
problematica, Amastra
pulchra, Leptachatina
pupoidea, Leptachatina
serrula, Auriculella
straminea, Auriculella
subovata, Leptachatina
tenebrosa, Carelia
thaanumi, Carelia paradoxa
thaanumi, Leptachatina
varia, Leptachatina
vetuscula, Amastra uniplicata

Cooke and Kondo

evelynae, Carelia
magnapustulata, Carelia paradoxa
moloaensis, Carelia olivacea
neckeri, Tornatellides
perantiqua, Partulina dubia
tsunami, Carelia pilsbryi

Cooke and Pilsbry

anceyana, Lyropupa
anceyana, Nesopupa
angusta, Nesopupa newcombi
antiqua, Lyropupa
attenuatus, Tornatellides
boettgeri, Pronesopupa
brunneus, Tornatellides
cylindrata, Lyropupa perlonga
cyrta, Lyropupa
dispersa, Nesopupa
dubitabilis, Nesopupa
filocostata, Lyropupa perlonga
fossilis, Lyropupa lyrata
gnampta, Nesopupa newcombi
hystricella, Pronesopupa
illibata, Tornatellaria sykesii
interrupta, Nesopupa newcombi
irregularis, Tornatellides
kaalaensis, Nesopupa dubitabilis
kahoolavensis, Tornatellides
lanceolata, Tornatellina
leptospira, Tornatellides
littoralis, Nesopupa
micra, Lyropupa
minuta, Auriculella
oahuensis, Nesopupa
oahuensis, Tornatellides
orycta, Pronesopupa
ovatula, Lyropupa
rhabdota, Lyropupa
rhadina, Nesopupa wesleyana
ronaldi, Tornatellides
singularis, Nesopupa
spaldingi, Lyropupa
spaldingi, Tornatellides
spinigera, Pronesopupa boettgeri
subcentralis, Nesopupa
sykesii, Tornatellaria
thaanumi, Lyropupa
thaumasia, Lyropupa
tryphera, Nesopupa wesleyana
virgula, Tornatellides
waianaensis, Nesopupa

Gould, Addison Augustus

acuminata, Achatinella [*Leptachatina*]
adusta, Achatina [*Carelia*]

canella, Succinea
caperata, Vitrina
cepulla, Succinea [*Helisaga*]
cerealis, Achatinella [*Leptachatina*]
cicercula, Helix [*Corasia*]
cryptoportica, Helix [*Corasia*]
ellipsoidea, Achatinella
exaequata, Helix [*Microcystis*]
explanata, Succinea [*Omalonyx*]
fornicata, Helix
fulginosa, Achatinella
guttula, Achatinella [*Leptachatina*]
lumbalis, Succinea
lyrata, Pupa [*Vertigo*]
microstoma, Achatinella
nacca, Vertigo
nucleola, Achatinella
pauxillus, Helix
peponum, Pupa [*Tornatellina*] [*Leptinaria*]
pusillus, Helix
radiata, Achatinella
reticulata, Physa
rubens, Achatinella
rubiginosa, Helix
setigera, Helix [*Pitys*]
stellula, Helix [*Pitys*]
striatula, Achatinella [*Leptachatina*]
subtilissima, Helix [*Zonites*]
tenella, Vitrina
uberta, Helicina
venusta, Succinea
vesicalis, Succinea
volutata, Limnea

Gulick, John Thomas

albescens, Achatinella
ampulla, Achatinella
analoga, Achatinella
baileyana, Achatinella
bulbosa, Achatinella
caesia, Achatinella
carinata, Amastra
cervina, Achatinella
cognata, Achatinella
concidens, Achatinella
coniformis, Apex
contracta, Achatinella
corrugata, Achatinella
costulata, Achatinella
crocea, Achatinella
crystallina, Achatinella
cucumis, Achatinella
decorticata, Amastra
delta, Achatinella
dimorpha, Achatinella
diversa, Achatinella
eburnea, Achatinella
elliptica, Amastra
exilis, Achatinella
fasciata, Achatinella
flavidus, Apex
formosa, Achatinella
fragilis, Achatinella
fumida, Achatinella
fuscula, Achatinella
glauca, Achatinella
granifera, Achatinella
gummea, Achatinella
herbacea, Achatinella
induta, Achatinella
juncea, Achatinella
lacrima, Achatinella
lactea, Achatinella
lagena, Achatinella
leucochila, Achatinella
leucophaeus, Apex
leucorrhaphe, Apex
leucozonus, Apex
lignaria, Achatinella
lilaceus, Apex
limbata, Achatinella
mahogani, Achatinella
marginata, Achatinella
nympha, Achatinella
obliqua, Achatinella
octogyrata, Achatinella
oomorpha, Achatinella
papyracea, Achatinella
parvula, Achatinella
petila, Achatinella
pexa, Achatinella
phaeozona, Achatinella
platystyla, Achatinella
plumata, Achatinella
plumbea, Achatinella
polymorpha, Apex
pyramidalis, Achatinella
resinula, Achatinella
rotunda, Achatinella
rubida, Amastra
rustica, Amastra
saxatilis, Achatinella
scitula, Achatinella
spadicea, Achatinella
stiria, Achatinella
striatella, Achatinella
subula, Achatinella
talpina, Achatinella
tenuilabris, Amastra
terebralis, Achatinella
torrida, Achatinella
trilineata, Achatinella
triticea, Achatinella
tuberans, Apex
tumefactus, Apex
turbiniformis, Apex
turrita, Achatinella
undosa, Achatinella
ustulata, Achatinella
varia, Achatinella
versicolor, Apex

versipellis, Achatinella
virens, Achatinella
vitreola, Achatinella
zonata, Achatinella

Hartman, William Dell

nattii 'Baldwin,' *Achatinella*

Hyatt, Alpheus

abberans, Amastra bigener
bigener, Amastra affinis
cindrella, Amastra affinis
rigida, Carelia
rubinia, Amastra rubens
subassimilis, Amastra assimilis

Hyatt and Pilsbry

borcherdingi, Amastra
hawaiiensis, Amastra
interjecta, Amastra soror
johnsoni, Amastra
media, Amastra textilis
orientalis, Amastra reticulata
semivestita, Laminella venusta
subcornea, Amastra
subcrassilabris, Amastra
subobscura, Amastra
subpolita, Partulina
subpulla, Amastra affinis
subsoror, Amastra

Jay, John Clarkson

bicolor, Achatina

Kondo, Yoshio

See under: Cooke and Kondo

Lea, Isaac

newcombii, Melania

Mighels, Jesse Wedgwood

accineta, Achatina
admodesta, Pupa
armatus, Bulimus
caduca, Succinea
cingula, Achatinella
clausinus, Bulimus
inornata, Achatinella
intercarinata, Helix
jugosa, Helix
laciniosa, Helicina
mustelina, Achatinella
nubilosa, Achatinella
patula, Succinea
picta, Achatinella
porrecta, Paludina
producta, Physa
pumicatus, Bulimus
rotelloidea, Helicina
scutilus, Bulimus
subrutila, Helix
tiara, Helix
turricula, Achatina
umbilicata, Physa
venusta, Achatinella
vestita, Achatinella
virgulata, Partula
viridans, Achatinella

Neal, Marie Catharine

globuloidea, Pleuropoma laciniosa
spaldingi, Pleuropoma laciniosa

Newcomb, Wesley

acuta, Achatinella
adamsi, Achatinella
affinis, Achatinella
agglutinans, Achatinella obesa
albolabris, Achatinella
alexandri, Achatinella
ampla, Achatinella
anthonii, Achatinella
aplustre, Achatinella
assimilis, Achatinella
baldwinii, Achatinella
biplicata, Achatinella
buddii, Achatinella
casta, Achatinella
cestus, Achatinella
concinna, Achatinella
cornea, Achatinella
crassa, Achatinella
crassilabrum, Achatinella
cumingi, Achatinella
curta, Achatinella
cylindrica, Achatinella
decipiens, Achatinella
dubia, Achatinella
dwightii, Achatinella
elegans, Achatinella
elongata, Achatinella
emmersonii, Achatinella
flavescens, Achatinella
fulgens, Achatinella
fumosa, Achatinella
fusca, Achatinella
fusoidea, Achatinella
germana, Achatinella
gigantea, Achatinella
glabra, Achatinella
gouldi, Achatinella
grana, Achatinella
grisea, Achatinella
helena, Achatinella
humilis, Achatinella
hybrida, Achatinella
intermedia, Achatinella
johnsoni, Achatinella

kauaiensis, Achatinella
labiata, Achatinella
lineolata, Achatinella
mastersi, Achatinella
mauiensis, Achatinella
melanosis, Achatinella
melanostoma, Achatinella
moesta, Achatinella
mucronata, Achatinella
multilineata, Achatinella
nigra, Achatinella
nitida, Achatinella
nivosa, Achatinella
obesa, Achatinella
obscura, Achatinella
ornata, Achatinella
ovata, Achatinella
petricola, Achatinella
pfeifferi, Achatinella
physa, Achatinella
polita, Achatinella
porcellana, Achatinella
porphyrea, Achatinella
pupoidea, Achatinella
pusilla, Achatinella
recta, Achatinella
redfieldi, Achatinella
remyi, Achatinella
reticulata, Achatinella
rubiginosa, Achatinella
rufa, Achatinella
rugosa, Achatinella
rutila, Achatinella
sanguinea, Achatinella
semicarinata, Achatinella
solitaria, Achatinella
sordida, Achatinella
soror, Achatinella
splendida, Achatinella
striata, Tornatellina
subvirens, Achatinella
succincta, Achatinella
swiftii, Achatinella
terebra, Achatinella
tessellata, Achatinella
tetrao, Achatinella
turgida, Achatinella
undulata, Achatinella
variabilis, Achatinella
venulata, Achatinella
violacea, Achatinella
vitrea, Achatinella
zebra, Achatinella

Pease, William Harper

ambigua, Limnaea
ambusta, Auriculella
angulata, Carelia adusta
antiqua, Leptachatina
bacca, Vertigo
balteata, Leptachatina
brevicula, Helicter
capillata, Helix
compacta, Helicter
compacta, Limnaea
compta, Helicter
contigua, Melania
costata, Vertigo
costulosa, Leptachatina
costulosa, Vertigo
cylindrata, Helicter
decussatula, Helix
dentata, Tornatellina
distans, Helix
elongata, Succinea
erecta, Helicter
expansa, Auriculella
extensa, Leptachatina
filocostata, Pitys
gracilis, Blauneria
gracilis, Tornatellina
hutchinsonii, Helicter
kauaiensis, Melania
laevis, Leptachatina
laminata, Helix
lucida, Leptachatina
lucidus, Melampus
neglecta, Neritina
oblonga, Tornatellina
olivacea, Carelia
pachystoma, Helicter
paucicostatus, Pithys
perlonga, Vertigo
porphyrostoma, Helicter
proximus, Helicter
pulchra, Auriculella
rubella, Succinea
rugata, Helix
rugulosa, Amastra
semiplicata, Melampus
similaris, Amastra rugulosa
simplex, Leptachatina
solida, Amastra
sphaerica, Amastra
striatula, Vertigo
tenebrosa, Leptachatina
tenuicostata, Helicter
triplicata, Auriculella
turgidula, Leptachatina
turgidula, Limnaea
uniplicata, Auriculella
variabilis, Carelia
viridis, Carelia variabilis

Pfeiffer, Ludwig

apicata 'Newcomb,' *Achatinella*
bicolor 'Gulick,' *Achatinella*
citrina 'Mighels,' *Achatinella*
cumingiana, Spiraxis
hystrix 'Mighels,' *Helix*
maniensis 'Newcomb,' *Achatinella*

plicata 'Mighels,' *Achatinella*
pyramis, Achatinella

Pilsbry, Henry Augustus

abavus, Amastra
aemulator, Amastra
baldwiniana, Amastra
cookei, Leptachatina
honomuniensis, Newcombia cinnamomea
hyattiana, Carelia
hyperleuca, Carelia bicolor
kuhnsi, Partulina
litus, Pterodiscus alatus
longior, Partulina terebra
makawaoensis, Amastra
sykesi, Amastra
thaanumi, Pterodiscus
thaanumiana, Partulina
wailauensis, Amastra violacea
wheatleyana, Achatinella elegans

Pilsbry and Cooke

acicula, Tornatellides perkinsi
alpha, Helicina laciniosa
anceyanum, Elasmias
arenarum, Amastra umbilicata
aurantium, Laminella gravida
aurora, Amastra obesa
auwahiensis, Amastra subsoror
avus, Leptachatina oryza
balteata, Partulina helena
berniceia, Helicina
beta, Helicina laciniosa
cacuminis, Auriculella diaphana
candida, Partulina horneri
decorata, Newcombia cinnamomea
delta, Helicina laciniosa
dextroversa, Achatinella sowerbyana
disjuncta, Nesopupa newcombi
duplocincta, Achatinella apexfulva
eos, Amastra
errans, Partulina physa
fuscospira, Partulina horneri
fuscozonata, Partulina horneri
gamma, Helicina laciniosa
gouldi, Lyropupa lyrata
gulickiana, Achatinella lehuiensis
interrupta, Lyropupa perlonga
juddii, Helicina
kahakuloensis, Amastra baldwiniana
kahoolavensis, Lyropupa
kahukuensis, Tornatellides
kailuanus, Tornatellides procerulus
kalamauensis, Amastra
kalihiensis, Laminella gravida
kaluaahacola, Partulina virgulata
kamaloensis, Laminella depicta
kamaloensis, Partulina redfieldii
kauensis, Amastra melanosis
kaunakakaiensis, Amastra
kona, Lyropupa ovatula
konana, Partulina physa
lahainana, Amastra
lanaiensis, Nesopupa baldwini
leucoderma, Laminella sanguinea
metamorpha, Amastra
moomomiensis, Amastra humilis
multistrigata, Partulina theodorei
nematoglypta, Leptachatina
nubigena, Amastra
oahuensis, Helicina
occidentalis, Partulina dwightii
pellucida, Auriculella auricula
percostata, Lyropupa micra
puukolekolensis, Lyropupa kahoolavensis
roseoplica, Achatinella sowerbyana
sepulta, Amastra humilis
simulator, Achatinella cestus
subpolita, [*Partulina*]
thaanumi [formerly *thaamuni*], *Achatinella*
thwingi, Partulina
ualapuensis, Newcombia cinnamomea
ultima, Amastra
waianaensis, Laminella gravida
wailauensis, Newcombia canaliculata

Reeve, Lovell Augustus

abbreviata, Achatinella
castanea, Achatinella
cochlea, Achatina
prasinus, Achatinella
producta, Achatinella
vittata, Achatinella

Smith, Edgar Albert

albospira, Apex
augusta, Achatinella
brunnea, Auriculella
concolor, Achatinella
conicospira, Amastra
conifera, Amastra
consanguinea, Achatinella
crassula, Auriculella
diaphana, Auriculella
fuscobasis, Bulimella
fuscolineata, Achatinella
fuscozona, Achatinella
gulickii, Apex
lehuiensis, Achatinella
malleata, Amastra
nigrolabris, Amastra
nucula, Amastra
perpusilla, Auriculella
pygmaea, Achatinella
tenuis, Auriculella
tricolor, Achatinella

Sykes, Ernest Ruthven

arborea, Leptachatina
henshawi, Leptachatina
perkinsi, Newcombia

Welch, D'Alte Aldrich

albalabia, Achatinella bulimoides
arnemani, Achatinella bulimoides
caesiapicta, Achatinella bulimoides
kaipapauensis, Achatinella bulimoides
oswaldi, Achatinella bulimoides
rosealimbata, Achatinella bulimoides

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The American orb weavers of the genera *Mecynogea, Manogea, Kapogea* and *Cyrtophora* (Araneae: Araneidae)

HERBERT W. LEVI

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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THE AMERICAN ORB WEAVERS OF THE GENERA *MECYNOGEA, MANOGEA, KAPOGEA* AND *CYRTOPHORA* (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. Nine species of *Mecynogea* are known, of which five are new: two from Mexico, one from Colombia, one from Brazil, and one apparently widespread from Venezuela to Mato Grosso state, Brazil. For the common southeastern North American *Mecynogea lemniscata,* new records are given from southern Brazil to northern Argentina. *Manogea* is a new genus with the common and widespread type species *M. porracea* and two new species, one in Central America, the other in northern Colombia and Venezuela. The four widespread American species previously placed in *Cyrtophora* are here placed in a new genus, *Kapogea.* These four species are difficult to distinguish using the genitalia as characters. The Old World *Cyrtophora citricola* has recently been found in Colombia, where it damages trees. There are 17 new synonyms.

INTRODUCTION

This is one of a series of revisions of the Neotropical orb weaver genera. Previous publications are cited in Levi (1993, 1996). In preparation are a key to the known genera of the American araneid orb weavers and revisions of the remaining unrevised araneid genera: *Cyclosa, Molinaranea, Mastophora, Agathostichus, Mangora, Eustala* and *Verrucosa.*

The orb weavers placed in the genera *Mecynogea* and *Cyrtophora* form a distinct group in the family Araneidae: their webs are horizontal, often dome-shaped, and supported by a tangled webbing. They are believed to lack viscid silk in the web (Kovoor and Lopez, 1982), and the dome has an extremely small, dry silk mesh (Plates 1, 2). Unlike other orb weavers, they do not reconstruct the web on a daily basis and may not remove old webs, but build a new one above the old (Plate 2C) (Lubin, personal communication). Whereas their silk glands differ from those of other araneids (Kovoor and Lopez, 1982, 1988), the external appearance of these spiders is not as distinct from other araneids as one might expect. Differences in their spinnerets are described by Coddington (1989) and Peters (1993). Peters also showed a secondary loss of some silk spigots in older spiders.

There is literature (Carico, 1984; Hieber, 1984) on the behavior and ecology of the basilica spider, *Mecynogea lemniscata,* and a recent paper by Willey et al. (1992) cites previous papers. Wise (1993), in his volume on the ecology of spiders, has many citations for *Mecynogea lemniscata.* The *Zoological Record* cites numerous papers on several *Cyrtophora* species. However, there is no literature on *Manogea* species, presumably because of the past difficulty of identifying the common *M. porracea,* and there is no literature on the species of *Kapogea,* which are less often collected despite the large size of females.

I am obliged to the curators and their assistants for making the collections available. I also thank M. E. Galiano for specimens (deposited in MACN) and C. L. Scioscia and P. Vanzolini for locating collecting sites. J. Carico, W. Eberhard, C. Hieber, Y. Lubin, N. C. Mesa C. and M. Robinson provided information on habits of the spiders. J. Coddington and Y. Lubin provided photographs. I am thankful to L.

[1] Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, Massachusetts 02138.

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METHODS

The methods used have been described previously (Levi, 1993).

The distances between eyes of the anterior row are expressed as diameters of the anterior median eyes (in profile); distances between eyes of the posterior row are given as diameters of the posterior median eyes (in profile). The height of the clypeus (the distance between anterior median eyes and the edge of the carapace) is measured by the diameter of the anterior median eye (Levi, 1993, fig. 28f). These measurements are approximate. The median eye quadrangle is delineated along the outer margins of the median eyes.

In preserved specimens the abdomen is held at an angle to the prosoma. Because this angle is variable, depending on the condition of the specimen, measurements of total length were made with the anterior of the abdomen slightly pushed down. The total length is thus an approximation. Illustrations of the dorsal view were made with both prosoma and opisthosoma horizontal.

The male palpi, because they are softer than those of many other araneids, were expanded by immersion in 10% sodium hydroxide solution in water, followed by immersion in distilled water. The expanded palpi of many other araneids, described in previous papers, were often just pulled apart with needles.

MATERIALS

Collections Examined. The spiders studied here were made available from the following collections:

ACCH Academia de Ciencias de Cuba, La Habana, Cuba (L. F. de Armas)

AMNH American Museum of Natural History, New York, United States (N. Platnick, L. Sorkin)

BMNH Natural History Museum, London, England (P. Hillyard, F. Wanless)

CAS California Academy of Sciences, San Francisco, California, United States (W. J. Pulawski, D. Ubick, C. Griswold)

DU D. Ubick, San Francisco, California, United States

FSCA Florida State Collection of Arthropods, Gainesville, Florida, United States (G. B. Edwards)

INPA Instituto Nacional de Pesquisas da Amazônia, Manaus, Est. Amazonas, Brazil (E. H. Buckup, H. Höfer)

IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (L. Baert)

JVN J. Vasconcellos-Neto, Campina, São Paulo, Brazil

MACN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (E. A. Maury, M. E. Galiano, C. L. Scioscia)

MCN Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil (E. H. Buckup, M. A. L. Marques)

MCP Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil (A. A. Lise)

MCZ Museum of Comparative Zoology, Cambridge, Massachusetts, United States

MECN Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador (L. Avilés, Germania Estévez J.)

MLP Museo de Universidad Nacional, La Plata, Argentina (R. F. Arrozpide, C. Sutton)

MNHN Muséum National d'Histoire Na-

turelle, Paris, France (J. Heurtault, C. Rollard)

MNRJ Museu Nacional, Rio de Janeiro, Brazil (A. Timotheo da Costa, Adriano Brilhante Kury)

MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (D. Silva D.)

MZSP Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil (P. Vanzolini, J. L. Leme, R. Pinto da Rocha)

MZUF Museo Zoologico de "La Specola" Università di Firenze, Florence, Italy (S. Whitman)

NMB Naturhistorisches Museum, Basel, Switzerland (A. Hänggi)

NRMS Naturhistoriska Riksmuseet, Stockholm, Sweden (T. Kronestedt)

PAN Polska Akademia Nauk, Warszawa, Poland (J. Prószynski, A. Slojewska, W. B. Jedryczkowski, T. Huflejt)

SMF Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (M. Grasshoff)

USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., United States (J. Coddington, S. F. Larcher)

ZSM Zoologische Staatssammlung, Munich, Germany

RELATIONSHIPS

Mecynogea and two of the three species here placed in *Manogea* differ from most other orb weavers by having a procurved posterior eye row as in *Argiope* and *Gea*. The posterior lateral eyes are anterior to the posterior medians (Figs. 1, 20). Is this homoplasy? One species of *Manogea, M. porracea* (Figs. 79, 88), and the four species of *Kapogea* (Figs. 107, 118), have the posterior eye row straight. The remaining araneid orb weavers, including most *Cyrtophora* species (which are related to *Mecynogea* and *Kapogea* by their unusual spinning habits), have the eyes of the posterior row recurved, the lateral eyes posterior to the medians (Fig. 152; Table 1).

Another character, perhaps more unusual, combines these three genera and *Cyrtophora* and may place them with *Argiope* and *Gea*. In all, the femur of each leg is about the same length as the combined patella and tibia of the same leg: the first slightly shorter, the second about the same, the third and fourth slightly longer. Also, the combined metatarsus and tarsus is longer than the combined patella and tibia of the same leg. In other words, the patellae and tibiae of this group are relatively shorter than in all other araneid genera (Table 1).

The hooded epigynum of *Mecynogea* (Fig. 5; [6] in Table 1) resembles that of *Argiope aurantia* Lucas (Levi, 1968, fig. 49; [10] in Table 1), and the lobed epigynum of other *Mecynogea* (Figs. 55–61) resembles *Argiope trifasciata* (Forskål) (Levi 1968, figs. 68, 69).

All evidence points to a clade embracing *Mecynogea, Manogea, Kapogea, Cyrtophora* and *Argiope* and *Gea*.

TAXONOMIC SECTION

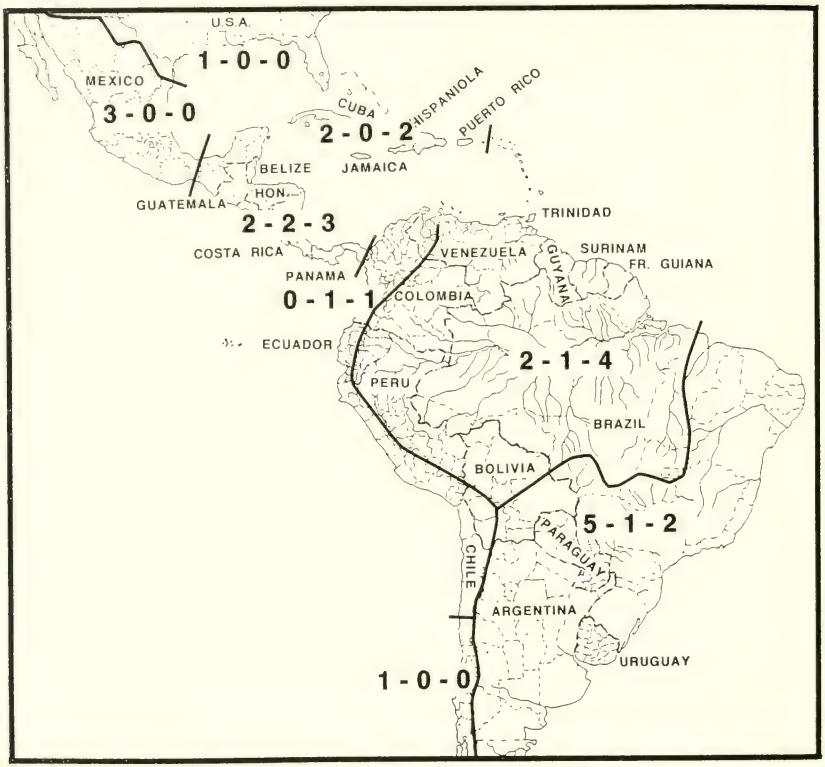
Mecynogea Simon

Hentzia McCook, 1894: 244. Type species by monotypy *Epeira basilica* McCook (=*M. lemniscata*). Name preoccupied by *Hentzia* Marx, 1883.

Mecynogea Simon, 1903: 25. Type species *M. bigibba* designated by Petrunkevitch, 1911: 360. Neave, 1940: 679. Roewer, 1942: 747. The gender of the name is feminine (Bonnet, 1957: 2744).

Allepeira Banks, 1932: 23. New name to replace *Hentzia* McCook, preoccupied. First synonymized with *Mecynogea* by Levi, 1980: 11.

Diagnosis. Mecynogea differs from most araneid orb weavers (including *Kapogea* and *Cyrtophora*) by having the posterior row of eyes procurved (Figs. 1, 15, 20), the lateral eyes anterior to the medians in dorsal view, as in *Gea* and *Argiope*. *Mecynogea* differs from *Gea* and *Argiope* by having a cylindical to oval abdomen with a pair of anterior dorsal tubercles (Figs. 15, 17; Table 1) and having three dark bands on the yellowish carapace (Figs. 1, 20), whereas in *Gea* and *Argiope* the abdomen



Map 1. The number of species of the three genera: first number *Mecynogea* species, second *Manogea* species, third *Kapogea* species.

is oval to shield-shaped (Levi, 1968, figs. 36, 52, 61), is dorsoventrally flattened, and often has transverse bands and the carapace without longitudinal bands. *Mecynogea* differs from *Manogea* by having the dorsal abdominal bands wavy at the middle of the abdomen (Figs. 15, 17, 31, 37, 51, 52, 76; Table 1), whereas in *Manogea* the bands are straight but disappear anteriorly (Figs. 85, 97, 103).

The epigynum of *Mecynogea* differs from that of *Manogea* by having a round hood with a large posterior opening (Figs. 4–6, 26, 27) or a sclerotized, projecting posterior median plate with the ducts opening in slits (Figs. 55–57, 59–61, 67–69, 73–75; [6] in Table 1), whereas *Manogea* has a pair of distinct openings in a cup-like structure (Figs. 82–84, 94–96, 100–102; [7] in Table 1). The male palpus of *Mecynogea* has a two-branched structure, considered the terminal apophysis, covering the embolus (Figs. 21, 22, A in Figs. 24, 25), the proximal branch (PB) covering part of the medial side and the distal branch (DB) covering the distal side

Table 1. Some characters belonging to the genera revised here with *Argiope* and *Alpaida*.[a]

	MEC[c]	MAN	KAP	CYR	ARG	ALP
Female[b]						
A line and 2 dark areas on carapace	+	+	−	−	−	−
Ceph. region width < 0.5 thorac. region	+	+	−	−	+	−
Lateral groove betw. ceph. & thorac. region	−	−	+/−	+/−	+/−	+
ALE facing venter	−	−	−	−	[+]	−
PE row procurved	+	+/−	−	−	+	−
PE row straight	−	−/+	+	−/+	−	−
PE row recurved	−	−	−	+/−	−	+
AME closer to ALE than each other	+	+/−	−	−	−	−
PME equally spaced	+	+	−	−	−	−
LE on small tubercle	−	−	+	+	+	−
LE separated by 0.5 Ø +	−	−	+	+	−	−
Ocul. quadrangle longer > wide	+	+	+	+	+	−
Femur i >/= patella + tibia	+/−	+	−	−	−	−
Femur iii, iv >/= patella + tibia	+	+	+	+	+	−
Metatarsus + tarsus > patella + tibia	+	+	+/−	+	+	−
Legs thick	−	−	+	+	−	−
Abdomen shape	1	1	[2]	[3]	[4]	[5]
Abdomen with straight longitudinal bands	−	[+]	−	−	−	−
Abdomen with wavy longitudinal bands	[+]	−	−	−	−	−
Epigynum structure	[6]	[7]	[8]	[9]	[10]	[11]
Aggregate silk glands	small	−	−?	−	+	+
Flagelliform silk glands	−	−	−?	−	+	+
Male						
Ceph. region width < 0.5 thorac. region	+	+	−	−	+	+
PE row procurved	+	−/+	−	−	+	−
PE row straight	−	+/−	+	−/+	−	−
AME closer to LE than each other	+	+	+	+	+	−
PME equally spaced	+	+	+/−	−	−	−
LE separated by 0.3 Ø +	−	−	+	+	−	−
ALE faces ventrally	−	−	−	−	[+]	−
Femur i longer > patella + tibia	−	−	−	−	−	−
Femur iii/iv >/= patella + tibia	+	+/−	+	+	+	−
Tarsus + metatarsus >/= patella + tibia	+	+	+	+	+	−
Legs thick	−	−	+	+	−	−
Abdomen shape	1	1	[2]	[3]	[4]	[5]
Abdomen with straight longitudinal bands	−	[+]	−	−	−	−
Abdomen with wavy longitudinal bands	[+]	−	−	−	−	−
Endite tooth	−	+/−	−	−	−	+
One palpal patellar seta	+	+	+	+	+	+
Hook on coxa i	−	−	−	−	−	+
Male length as % length of female	70–107	58–76	<24	18	35–50	100
A biforked	[+]	−	−	−	−	−
M small, soft	[−]/+	+	+	+	−	−
Embolus support	A	A	A	C	C	C

[a] Genera: ALP, *Alpaida*; ARG, *Argiope*; CYR, *Cyrtophora*; KAP, *Kapogea*; MAN, *Manogea*; MEC, *Mecynogea*.

[b] Abbreviations: A, terminal apophysis; ALE, anterior lateral eyes; AME, anterior median eyes, C, conductor; ceph., cephalic; LE, lateral eyes; M, median apophysis; ME, median eyes; ocul., ocular; PE, posterior eyes; PME, posterior median eyes; betw., between; thorac., thoracic.

[c] Codes: >, longer than; <, less than; >/=, longer or equal; =, same; +, present; −, absent; −/+, absent, present in some species; Ø, diameter; [ ], synapomorphy for the species included in the genus; ?, not known.

of the palpus (Figs. 24, 25), whereas *Manogea* has a soft terminal apophysis.

Description. Females. Coloration similar in all species. Carapace yellowish, with three dark bands (Figs. 1, 20). Chelicerae yellowish, labium and endites brown. Sternum brown with an irregular median, longitudinal light band. Legs yellowish, femora with longitudinal dark lines, distal articles with indistinct dark rings. Abdomen dorsum with longitudinal bands that undulate in middle of abdomen (Figs. 15, 31, 52), venter blackish, with paired white bands, most anterior longest, most posterior a round patch on sides of spinnerets (Fig.16).

Cephalic region of carapace about half or less of maximum width of carapace (Figs. 1, 20). Eyes similar in size, but anterior median eyes slightly the largest, anterior laterals smallest, posterior medians and laterals intermediate (Figs. 1, 20). Anterior median eyes one diameter or slightly less apart, closer to laterals; posterior median eyes one diameter or slightly more apart, same distance from laterals (Figs. 1, 2, 18, 20). Ocular quadrangle wider in front than behind, quadrangle longer than wide in front (Figs. 2, 18, 20). Height of clypeus equals 0.4 to 0.8 diameter of anterior median eye (Fig. 2). Legs relatively long, with length of first patella and tibia almost twice width of carapace. First and second femora slightly shorter than accompanying patella and tibia; third and fourth slightly longer. All legs with metatarsus and tarsus longer than patella and tibia of same leg. Legs with short setae and with scattered, relatively long setae at right angles to axis of leg.

Males. Slightly larger or smaller than females and similar in structure and coloration. Height of clypeus as in female (Fig. 18). Endite tooth lacking, coxal hook lacking, palpal patella with one macroseta. Legs as in female.

Genitalia. Epigynum with median posterior lobe, an extension of median posterior sclerite (Figs. 55, 59, 67, 73, *M. ocosingo, M. buique, M. apatzingan*), triangular in shape (Fig. 73, *M. martiana*) or with dome-shaped hood hiding cavity with a large posterior facing opening (Figs. 4–6).

Male palpus with a pair of branches, perhaps homologous with the terminal apophysis, covering the distal and mesal sides of the palpus (A in Fig. 24). Median apophysis lost in males whose females have a hood-like epigynum, present in those lacking the hood: *M. apatzingan* (at 4h in Fig. 71, between center and 6h in Fig. 72), *M. martiana* (between center and 9h in Fig. 78) and *M. ocosingo* (at 4h in Fig. 63). Conductor on margin of tegulum (C in Fig. 25). Palpal tibia with several long setae.

Silk Glands. Mecynogea species lack flagelliform silk glands (which produce the axial thread of viscid silk) but, unlike species of *Manogea* and *Cyrtophora,* have small aggregate glands (producing viscid silk). The silk glands were studied in *Mecynogea lemniscata* and in *Manogea porracea* (=*Mecynogea guianensis*) by Kovoor and Lopez (1988).

Relationship. The horizontal, dome-shaped web (Plates 1A, B) and the absence of flagelliform silk glands allies *Mecynogea* with *Manogea, Kapogea* and *Cyrtophora,* as do the unusual leg lengths, the third and fourth femur being equal to or slightly longer than the patella and tibia of the same leg and all metatarsi and tarsi longer than the patella and tibia of the same leg. But *Manogea* and *Cyrtophora,* and probably also *Kapogea,* have lost their aggregate glands, which are still present but small in *Mecynogea.* Whereas small males of araneid species usually loose their endite tooth and coxal hook, *Mecynogea* males also lack them, despite being equal in size to females. *Argiope* lack these structures, but it is uncertain whether this loss is a synapomorphy with *Mecynogea* or convergence resulting from small male size. The unusual proportions of leg articles, relatively long femora, metatarsi and tarsi compared with the corresponding pa-

Plate 1. A, *Mecynogea bigibba* female hanging in web, from São Paulo. B, orb on bottom and eggsac in center of photograph of *Manogea porracea*, in Panama; in center are also orbs of uloborids.

tellae and tibiae, is also found in *Argiope* species.

Natural History. All *Mecynogea* species make a horizontal, dome-shaped web with small mesh and lacking viscid threads (Plate 1A), as do *Manogea* (Plate 1B), *Kapogea* (Plate 2C) and *Cyrtophora*. The common name "basilica spider" presumably reflects the domed design of the orb web.

Distribution. Mecynogea species are found only in the Americas (Maps 1, 2).

Separating Species. Because the general appearance of all species is the same, genitalia are used to distinguish species. Because the male palpi have less variation than the epigyna, males are easier to distinguish than females. Before males were found for South American *M. lemniscata* and *M. bigibba,* the females of both were considered to represent several species.

KEY TO FEMALE *MECYNOGEA*

1. Epigynum with bulging hood having a large opening facing posteriorly (Figs. 4, 5, 26, 27, 34, 35, 40, 41) 2
– Epigynum without hood (Figs. 55, 56, 59, 60, 67, 68, 73, 74) 5
2(1). Epigynum with notch on posterior margin of hood (Figs. 34, 35); Venezuela to Mato Grosso, Brazil (Map 2A) ..... *sucre*
– Rim of hood without notch (Figs. 4, 26, 40) 3
3(2). Slit-shaped openings of ducts visible dorsally within cavity of hood (bottom of Fig. 27, Figs. 41, 44) 4
– Slit-shaped openings not visible within cavity of hood (Figs. 5, 8, 11, 14); southeastern Brazil, Uruguay (Map 2C) .. *bigibba*
4(3). Slit-shaped openings of ducts visible along dorsal margin of hood opening; (Figs. 41, 44, 47, 50); bottom of cavity often with longitudinal ridge (Figs. 41, 44, 50); Maryland to Missouri, United States to northern Argentina (Map 2A) ..... *lemniscata*
– Slit-shaped openings of ducts on sides of triangular dorsal median plate (at 5h and 7h in Figs. 27, 30); bottom of depression with a longitudinal groove (Figs. 27, 30); Minas Gerais, Brazil, to Argentina and Chile (Map 2B) ..... *erythromela*
5(1). Epigynum of triangular shape, in ventral view, bearing a shallow transverse groove (Fig. 73); Cuba, Hispaniola (Map 2D) ..... *martiana*
– Epigynum otherwise (Figs. 55, 59, 67) 6
6(5). Epigynum in ventral view with a median lobe arising from below posterior margin (Figs. 59–61); Mexico (Map 2D) *ocosingo*
– Epigynum with median lobe arising from posterior of ventral plate (Figs. 55, 67) 7
7(6). Epigynum with median lobe about as wide as long (Fig. 67), posterior median plate a distinct sclerite (center of Fig. 68); central Mexico (Map 2D) ..... *apatzingan*
– Epigynum with median lobe wider than long (Fig. 55); posterior median plate an indistinct unbordered area (Fig. 56); Pernambuco, Brazil (Map 2A) ..... *buique*

KEY TO MALE *MECYNOGEA*

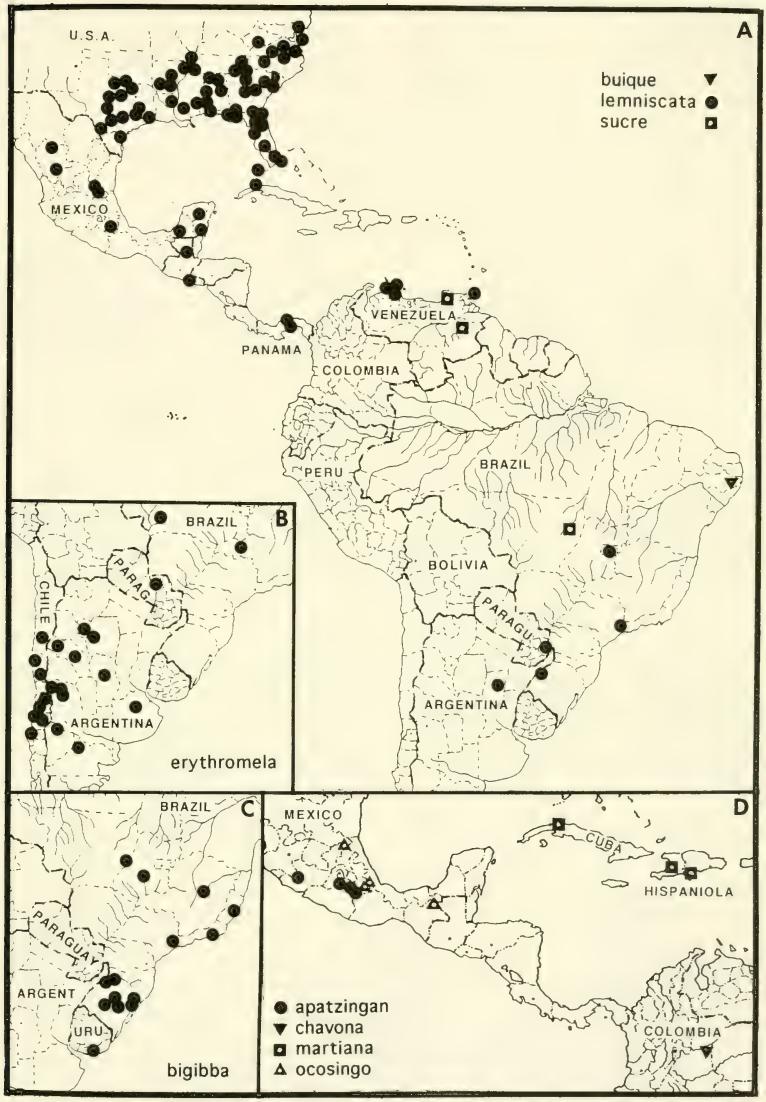
1. Proximal branch of terminal apophysis of palpus almost circular, covering most of palpus in mesal view (Fig. 32); Minas Gerais, to Argentina and Chile (Map 2B) ..... *erythromela*
– Both branches narrow (Figs. 21, 24, 38, 53, 65, 71, 77) 2
2(1). Distal branch of terminal apophysis in mesal view wider than proximal branch (Fig. 77); Cuba, Hispaniola (Map 2D) .. *martiana*
– Branches of similar width, or distal one narrower in mesal view (Figs. 21, 38, 53, 63, 65, 71) 3
3(2). Proximal branch with a deep notch on upper side, bordered by a lip (Fig. 53); Maryland to Missouri, United States to northern Argentina (Map 2A) ..... *lemniscata*
– Proximal branch without notch (Figs. 21, 38, 63, 65, 71) 4
4(3). Proximal branch distally rounded (Fig. 63); Depto. Meta, Colombia (Map 2D) ..... *chavona*
– Proximal branch pointed at end (Figs. 21, 38, 63, 71) 5
5(4). Median apophysis with spine (at 4h in Figs. 63, 71, below center of Figs. 64, 72) 6
– Without median apophysis (Figs. 21, 22, 38, 39) 7
6(5). In mesal view, distal branch of terminal apophysis with a distal depression (at 2h in Fig. 71); central Mexico (Map 2D) ..... *apatzingan*
– In mesal view, distal branch of terminal apophysis curved out (at 2h in Fig. 63); Mexico (Map 2D) ..... *ocosingo*
7(5). Thread-shaped embolus showing between two branches (Fig. 21, E in Fig. 24); southeastern Brazil, Uruguay (Map 2C) ..... *bigibba*
– Embolus not visible between branches of terminal apophysis (Fig. 38); Venezuela to Mato Grosso, Brazil (Map 2A) ..... *sucre*

Mecynogea bigibba Simon
Plate 1A; Figures 1–25; Map 2C

Mecynogea bigibba Simon, 1903: 25. Female holotype from Goyaz [Goiânia, Goias state], Brazil, in MNHN, examined. Roewer, 1942: 747. Bonnet, 1957: 2745.

Wixia infelix Soares and Camargo, 1948: 378. Female from Chavantina, Mato Grosso, Brazil, in MZSP no. 1300, examined. Brignoli, 1983: 281. NEW SYNONYMY.

Description. Female from São Paulo, Brazil. Coloration as in other species, but more contrasting (Figs. 15–17). Total length 7.2 mm. Carapace 2.9 mm long, 2.3



Map 2. Distribution of *Mecynogea* species.

wide in thoracic region, 1.1 wide behind posterior median eyes. First femur 4.0 mm, patella and tibia 4.2, metatarsus 3.5, tarsus 1.2. Second patella and tibia 3.2 mm, third 2.1, fourth 3.1.

Male from Rio de Janeiro. Coloration as in female. Total length 7.7 mm. Carapace 3.5 mm long, 2.5 wide in thoracic region, 1.1 wide behind posterior median eyes. First femur 5.6 mm, patella and tibia 5.8, metatarsus 5.7, tarsus 1.6. Second patella and tibia 4.5 mm, third 2.5, fourth 4.3.

Note. Males and females were collected together.

Variation. Total length of females 6.3 to 11.6 mm, males 4.8 to 7.7. The specimens illustrated in Figures 1–6 and 18–25 were from the São Paulo Botanical Gardens; Figures 7–9 from Espírito Santo; Figures 10–12 from Minas Gerais; and Figures 13 and 14 from Mato Grosso. It is assumed they are all one species, which can only be ascertained by finding males.

Diagnosis. Mecynogea bigibba females are distinguished from others by not showing slit-shaped openings into the ducts in ventral view of the epigynum; the slits are hidden underneath the lateral plates (Figs. 5, 8, 11, 14). Also, the epigynum has a hump in profile (Figs. 6, 9), and in posterior view the floor of the cavity has a bulge (center of Figs. 5, 8). The male of *M. bigibba* is distinguished from others by showing the thread-shaped embolus in the space between the two branches of the terminal apophysis (Fig. 21, E in Fig. 24) and by the wide distal branch as seen in ventral view (Fig. 22).

Natural History. Specimens were found in shrubbery close to a pond in São Paulo (Plate 1A).

Distribution. Southeastern Brazil, Uruguay (Map 2C).

Specimens Examined. BRAZIL *Minas Gerais:* Diamantina, 2 imm., 1♀, doubtful determination (MNRJ); Minas de Serrinha, Diamantina, Feb., Mar. 1945, 1♀ (E. Cohn, AMNH). *Espírito Santo:* M. Moscoso, Vitória, Oct. 1981,1♀ (A. Cerrutti, MNRJ). *Rio de Janeiro:* Sumare, Cidade Rio de Janeiro, Feb. 1946, 3♀ (H. Sick, AMNH); Grumari, Rio de Janeiro, Dec. 1970–Jan. 1971, 2 imm., 1♂ (D. McGrath, S. M. Camazine, MCZ). *São Paulo:* Jardim Botânico, 9,10 Mar. 1985, 3♀ (H., L. Levi, MCZ); Embú, 9,10 Feb. 1974, 1♀ (F. Lane, MZSP 4897); São Roque, 7 Mar. 1976, 1♀ (F. Lane, MZSP 11521). *Rio Grande do Sul:* Canoas, 24 Jan. 1991, 1♂ (M. A. L. Marques, MCN 20456); Cerro Claro, São Pedro do Sul, 11 Jan. 1985, 6♀, 2♂ (A. A. Lise, MCN 12921); Cordilheira Cachoeira do Sul, 30 Dec. 1993, 1♂ (R. G. Buss, MCP 4382); Montenegro, 1 July 1977, 12 imm., 3♀, 5♂ (H. Bischoff, MCN 7480); Parque Florestal Estadual de Nonoai, Nonoai, 14 Jan. 1985, 1♀ (A. A. Lise, MCN 12812); São Leopoldo, 28 Nov. 1965, 3 imm., 1♂ (C. Valle, MZSP 4897); Sobradinho, 10 Jan. 1985, 11 imm., 2♀, 2♂ (A. A. Lise, MCN 12884); Tenente Portela, 29 Nov. 1978, 1 imm, 1♀ (H. Bischoff, MCN 8426); Triunfo, 12 Jan. 1989, 1♀ (A. B. Bonaldo, MCN 18081); Viamão, Aquas Belas, 29 Dec. 1976, 1 imm., 1♂ (A. A. Lise, MCN 5862). URUGUAY Piriapolis, 10 Dec. 1966, 1♀ (R. M. Capocasale, L. Bruno, CAS).

Mecynogea erythromela (Holmberg) Figures 26–33; Map 2B

Zilla erythromela Holmberg, 1876: 80. Female specimen from Las Conchas, Argentina [Partido de Tigre, Prov. Buenos Aires, 34°25′S, 58°34′W (Paynter, 1995: 405)], lost. First placed in *Mecynogea* by Mello-Leitão, 1933: 33.

Mecynogea tucumana Simon, 1903: 25. Female holotype from Tucumán, Argentina, in MNHN, examined. Roewer, 1942: 747. Bonnet, 1957: 2745. NEW SYNONYMY.

Gea bimucronata Mello-Leitão, 1936: 125, fig. 14, ♀. Female from Constitutión, Maule, Chile, in MNRJ,

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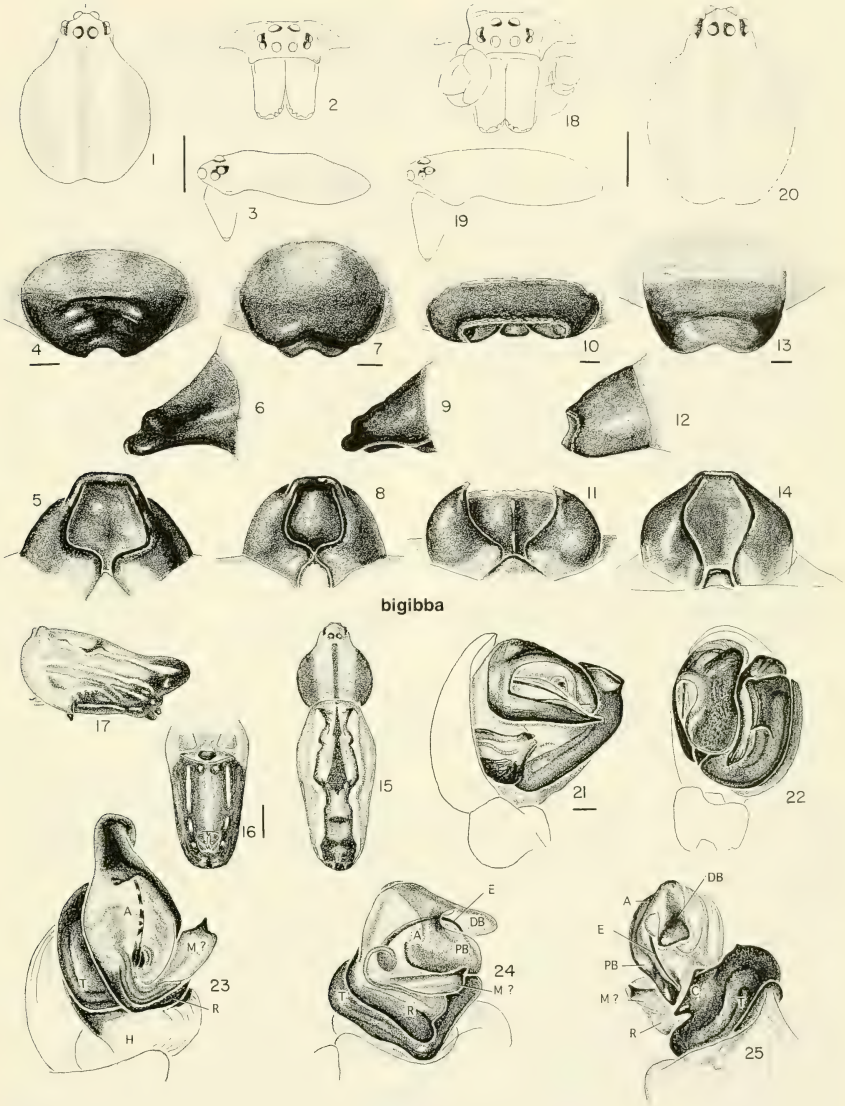
Figures 1–25. *Mecynogea bigibba* Simon. 1–17, female. 1, carapace; 2, eye region and chelicerae; 3, carapace and chelicera, lateral. 4–14, epigynum. 4, 7, 10, 13, ventral; 5, 8, 11, 14, posterior; 6, 9, 12, lateral. 4–6, (from São Paulo); 7–9, (from Espírito Santo); 10–12, (from Minas Gerais); 13, 14, (from Mato Grosso). 15, dorsal; 16, abdomen, ventral; 17, abdomen, lateral. 18–25, male. 18, eye region, chelicerae and right palpus; 19, carapace and chelicera, lateral; 20, carapace. 21–25, left male palpus. 21, mesal; 22, ventral; 23, expanded, subdorsal; 24, expanded, submesal; 25, expanded, subventral.

Abbreviations. A, terminal apophysis; C, conductor; DB, distal branch of terminal apophysis; E, embolus; H, hematodocha; M, median apophysis; PB, proximal branch of terminal apophysis; R, radix; T, tegulum.

Scale lines: genitalia 0.1 mm; others 1.0 mm.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bigibba
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examined. Roewer, 1942: 746. Bonnet, 1957: 1982. NEW SYNONYMY.

Mangora bituberculata Mello-Leitão, 1939: 63, figs. 34–37, ♂. Male from Paraguay, in NMB, examined. Roewer, 1942: 774. Bonnet, 1957: 2708. NEW SYNONYMY.

Mecynogea erythromela:—Roewer, 1942: 747. Bonnet, 1957: 2745.

Allepeira donosoi Archer, 1963: 17.

Note. Holmberg (1876) noted that he had only a poorly preserved female. His description of the closely spaced eyes, size and wavy abdominal bands fit this species; the description of the black and red color is less accurate; but a dry specimen may have been more red than the orange coloration noted in other descriptions. Simon's description lacked illustrations. The illustrations of *Gea bimucronata* are poor; those of *Mangora bituberculata* are of the male not previously associated with this species. Specimens and a citation of this species from Chile were labeled *Allepeira donosoi* by Archer, but no description has been found in the literature.

Description. Female from Mendoza. Coloration as in other species, dorsal abdominal bands relatively wide and less distinct. Total length 6.6 mm. Carapace 2.3 mm long, 1.7 wide in thoracic region, 0.7 wide behind median eyes. First femur 3.3 mm, patella and tibia 3.4, metatarsus 2.9, tarsus 1.2. Second patella and tibia 3.0 mm, third 1.8, fourth 2.7.

Male from Mendoza. Coloration as in female, but less distinct. Total length 3.8 mm. Carapace 1.7 mm long, 1.2 wide in thoracic region, 0.7 wide behind posterior median eyes. First femur 2.7 mm, patella and tibia 2.8, metatarsus 2.7, tarsus 1.0. Second patella and tibia 2.5 mm, third 1.2, fourth 2.0.

Note. Males and females were collected together.

Variation. Total length of females 5.6 to 7.5 mm, males 3.7 to 5.7. As in other *Mecynogea* species, there is considerable variation in the structure of the epigynum. The lateral plates, in posterior view, are long in Argentinean specimens (Fig. 27), shorter in females from Chile (Fig. 30).

Figures 26–28 were made from female holotype of *M. tucumana,* Figures 32 and 33 from a male from Mendoza, Argentina, and Figures 29 and 30 from the holotype of *Gea bimucronata* from Chile.

Diagnosis. Females of *M. erythromela* differ from other species by having the cavity of the epigynum hood with a median, longitudinal groove and expanding dorsally into the raised median plate (at 6h in Figs. 27, 29). The round terminal apophysis covering most of the palpus readily distinguishes males (Fig. 32).

Natural History. The collecting sites in Mendoza and in Santiago del Estero were in dry, chaparral-like shrubbery.

Distribution. Minas Gerais, Brazil, to Argentina and Chile (Map 2B).

Specimens Examined. BRAZIL *Mato Grosso:* Poconé, 4–10 Aug. 1992, 1♀ (A. A. Lise, G. A. Beaul, MCP). *Minas Gerais:* Reserva Ecológica do Parga, Uberlandia, 1 Sept. 1989, 1♂ (C. M. L. Ribeiro, MCP 1147). PARAGUAY *Concepción:* Territ. Fonciere [Fonciere], 1908, 2♀, 1♂ (E. Reimoser, MCZ). ARGENTINA *Santiago del Estero:* 70 km W Santiago, 3 Apr. 1965, 1♀, 1♂ (H. Levi, MCZ); Santiago del Estero, 2 Apr. 1965, 1♂ (H. Levi, MCZ). *Tucumán:* Tucumán, 1–15 May 1950, 3♀ (M. L. Aczél, AMNH); Cord. Valle Hermoso, Feb. 1958, 1♀ (O. de

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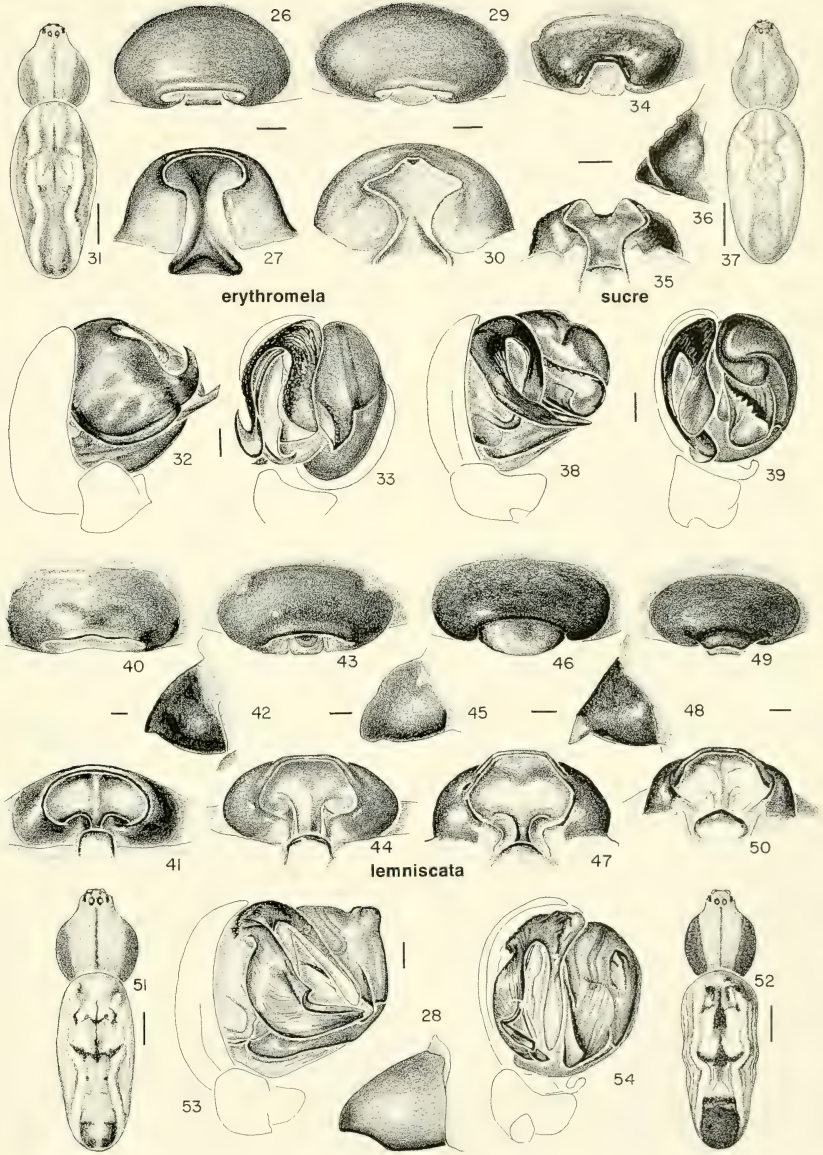
Figures 26–33. *Mecynogea erythromela* (Holmberg). 26–31, female. 26–30, epigynum. 26, 29, ventral; 27, 30, posterior; 28, lateral. 26–28, (from Argentina); 29–30, (from Chile). 32, 33, left male palpus. 32, mesal; 33, ventral.

Figures 34–39. *M. sucre* new species. 34–37, female. 34–36, epigynum. 34, ventral; 35, posterior; 36, lateral. 37, dorsal. 38, 39, male palpus. 38, mesal; 39, ventral.

Figures 40–54. *M. lemniscata* (Walckenaer). 40–52, female. 40–50, epigynum. 40, 43, 46, 49, ventral; 41, 44, 47, 50, posterior; 42, 45, 48, lateral. 40, 41, (from Panama); 43, 44, (from Venezuela); 46–48, (from Distrito Federal, Brazil); 49, 50, (from Argentina). 51, 52, dorsal. 51, (from Venezuela). 52, (from Argentina). 53, 54, male palpus. 53, mesal; 54, ventral.

Scale lines: genitalia 0.1 mm; others 1.0 mm.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Ferraris, AMNH). *La Rioja:* Cuesta de Miranda, Jan. 1964, 1♀, 1♂ (M. E. Galiano, MACN); Patquia, Jan. 1964, 1♀ (M. E. Galiano, MACN). *Córdoba:* Valle Hermoso, Feb. 1958, 1♀ (C. de Ferraris, AMNH). *Mendoza:* Mendoza, 900 m, Feb. 1908, 2♀ (E. Reimoser, MCZ). 30–31 Mar. 1965, 2 imm., 5♀, 1♂ (H. Levi, MCZ); Depto. Luján, S km SSW Estación Cachenta, 1500 m, Apr. 1958, 1♀ (B. Patterson, MCZ); Las Heras, 7 km W Mendoza, 1200 m, Mar., Apr. 1958, 5♀ (B. Patterson, MCZ). *Neuquén:* Butaco [21 km N Buta Ranquil], Jan. 1975, 3 imm., 1♀, 1♂ (E. Maury, MACN). *Río Negro:* Coronel Juan F. Gómez, Nov. 1945, 1♀ (I. Crasso, MLP). CHILE *Región III de Atacama:* Copiapó Sector, María Isabel, 6 Feb. 1982, 4♀, 11♂ (J. Moreno, AMNH). *Región IV de Coquimbo:* Fundo Tahuinco, Depto. Salamanca, 1 May 1961, 1♀ (A. F. Archer, AMNH). *Región Metropolitana:* Alhué, July 1947, 1♂ (L. Peña, IRSNB); Santiago, 17 Dec. 1988, 3♀, 1♂ (B., V. Roth, CAS). *Región VI del Libertador Gral. Bernardo O'Higgins:* Fundo Millahue Cunaco, Colchacua, 25 Mar. 1961, 2♀ (Donoso, A. F. Archer, AMNH). *Región VII de Maule:* Talco, 2♀ (MNRJ); Llico, 5♀ (L. Peña, IRSNB). *Región VIII del Bío-Bío:* Nueva Aldea, 10 Jan. 1976, 10♀, 4♂ (G. Moreno, AMNH).

Mecynogea sucre new species
Figures 34–39; Map 2A

Holotype. Male holotype and female paratype from 7 km E of San Antonio del Golfo, Sucre, Venezuela, 23 Mar. 1982 (G. F., J. F. Hevel), in USNM. The specific name is a noun in apposition after the locality.

Description. Female paratype. Carapace yellowish with black pigment, poorly preserved. Abdomen banded (Fig. 37) but with little black pigment; venter with a pair of white lines, broken into three parts, anterior longest, posterior shortest, black only outside their border. Height of clypeus equals 0.4 diameter of anterior median eye. Total length 5.6 mm. Carapace 2.0 mm long, 1.4 wide in thoracic region, 0.8 wide behind posterior median eyes. First femur 2.7 mm, patella and tibia 2.6, metatarsus 2.3, tarsus 0.9. Second patella and tibia 2.3 mm, third 1.4, fourth 2.3.

Male holotype. Carapace with median black line, only little black pigment on sides of thoracic region. Coloration as in female. Height of clypeus equals 0.4 diameter of anterior median eye. Total length 4.3 mm. Carapace 1.9 mm long, 1.5 wide in thoracic region, 0.7 wide behind posterior median eyes. First femur 2.6 mm, patella and tibia 2.9, metatarsus 2.6, tarsus 0.1. Second patella and tibia 2.6 mm, third 1.4, fourth 2.3.

Note. Males and females were collected together.

Variation. Total length of females 5.5 to 5.7 mm. The illustrations were made from holotype and female paratypes.

Diagnosis. The notch on the posterior margin of the epigynum hood (Figs. 34, 35) distinguishes the female from those of other species. The openings to the ducts are not visible in posterior view. The male is distinguished from others by having the long axis of the distal branch of the embolus branch almost parallel to the long axis of the cymbium, its tip covered by the proximal branch (Fig. 38).

Natural History. Specimens came from marsh-lake area in Bolívar state, Venezuela.

Distribution. Venezuela to Mato Grosso, Brazil (Map 2A).

Specimens Examined. VENEZUELA *Bolívar:* 40 km N Guasipati, 22 Mar. 1982, 1 imm., 1♀, 1♂ (G. F., J. F. Hevel, USNM). BRAZIL *Mato Grosso:* 260 km N Xavantina, 12°49′S, 51°46′W, 400 m, Feb., Apr. 1969, 1♀ (Xavantina-Cachimbo Expedition, MCZ).

Mecynogea lemniscata (Walckenaer)
Figures 40–54; Map 2A

Linyphia lemniscata Walckenaer, 1841: 263. Name for illustration fig. 25, j, Abbot, 1792, The Insects of Georgia in America, in BMNH. Photocopy in MCZ, examined.

Argiope trivittata O. P.-Cambridge, 1889: 51, pl. 4, fig. 5, ♂ [not fig. 6, ♀]. Syntypes from Dolores [?], Sacrixpur [?], betw. Dolores and Chapallal [?] and San José River nr. Chiquimuh [Chicimula], Guatemala, in BMNH. Male lectotype, designated by F. P.-Cambridge, 1904: 523, not female paralectotypes. NEW SYNONYMY.

Epeira basilica McCook, 1878: 133, figs. 1–3, ♀. Lectotype from Austin River, Texas, designated by Levi (1980).

Hentzia trivittata:—F. P.-Cambridge, 1904: 523, pl. 51, fig. 12, ♂ [not fig.13, ♀]. Bonnet, 1957: 2157.

Allepeira basilica:—Roewer, 1942: 778.

Allepeira trivittata:—Roewer, 1942: 778.

Gea wiedenmeyeri Schenkel, 1953: 17, fig. 15, ♀. Female holotype from Pozón, Prov. Falcón, Venezuela, in NMB, examined. Brignoli, 1983: 244. NEW SYNONYMY.

Allepeira affinitata Kraus, 1955: 26, figs. 54–56, ♀,

♂. Male holotype from El Salvador, in SMF, examined. Synonymized by Levi (1980).
Hentzia basilica:—Bonnet, 1957: 2157.
Mecynogea lemniscata:—Levi, 1980: 13, pl. 1, figs. 1–15. ♀, ♂.
Mecynogea affinitata:—Brignoli, 1983: 274.

Description. Female holotype of *M. wiedenmeyeri.* Coloration as in others, but anterior of dorsum of abdomen lighter and less distinctly marked (Fig. 51). Total length 7.9 mm. Carapace 3.3 mm long, 2.5 wide in thoracic region, 1.3 wide behind posterior median eyes. First femur 4.6 mm, patella and tibia 4.7; metatarsus , tarsus lost. Second patella and tibia 4.0 mm, third 2.5, fourth 4.0.

Male. From Garruchos, Rio Grande do Sul, Brazil. Coloration as in female (Figs. 51, 52). Total length 6.0 mm. Carapace 2.6 mm long, 1.9 wide in thoracic region, 0.9 wide behind posterior median eyes. First femur 3.8 mm, patella and tibia 4.2, metatarsus 3.9, tarsus 1.4. Second patella and tibia 3.9 mm, third 2.0, fourth 3.1.

Variation. Total length of females 7.5 to 10.5 mm, males 4.5 to 7.3. The shape of the hood openings are variable. Figures 40–42, were made from a female from Panama; Figures 43–45, from the holotype of *Gea wiedenmeyeri* from Venezuela; Figures 46–48 and 51 from a female from Distrito Federal, Brazil; Figures 49, 50 and 52 a female from Argentina; and Figures 53 and 54 from a male from Yucatán, Mexico.

Diagnosis. The openings to the ducts in the epigynum are in slits within the hood opening, ventral and median to the lateral plates (at 4h and 6h in Figs. 41, 44, 47, 50), those of *M. bigibba, M. erythromela* and *M. sucre* are hidden underneath the lateral plates (Figs. 8, 27, 35). In *M. lemniscata,* unlike *M. erythromela,* the cavity has a longitudinal, median ridge (Figs. 41, 50). The notch with a lip on the distal surface of the proximal branch of the terminal apophysis (Fig. 53) readily distinguished the male from those of other species.

Distribution. Maryland to Missouri, United States, to northern Argentina (Map 2A). The map includes data from Levi (1980).

Specimens Examined. BAHAMA ISLANDS *South Bimini:* July 1951, 1♂ (C., P. Vaurie, AMNH). LESSER ANTILLES *Trinidad:* Gasparee, 5 Nov. 1946, 1♀ (R. H. Montgomery, AMNH). *Curaçao:* Fuik (Oostpunt), 26 Dec. 1962, 1♂, fragments with palpus from mud dauber nest (H. Levi, B. de Jong, MCZ). MEXICO *San Luis Potosí:* Valles, 1961, 2♀, 1♂ (L. Steude, AMNH); 3 km W Pilares, 21 Oct. 1994, 1♀ (W. Piel, MCZ). *Durango:* Durango, 4 Aug. 1954, 1♂ (W. J. Gertsch, AMNH). *Campeche:* 6 km W Francisco Escarcega, El Tormento forest station, 11, 12 July 1983, 2♂ (W. Maddison, MCZ). *Yucatán:* Chichén Itzá, 1♀ (C. J. Goodnight, AMNH); 28 June 1975, 1♂ (W. Sedgwick, MCZ). *Quintana Roo:* Chetumal, 28 June 1975, 1♂ (W. Sedgwick, MCZ). PANAMA *Panamá:* Cerro Galero, 15 July 1985, 1♀ (W. Eberhard, MCZ); Fort Kobbe, 3 Aug. 1983, 1♀ (H., L. Levi, H. Stockwell, MCZ). VENEZUELA *Falcón:* Paraguana Península, ca. 6 km W Nuevo Pueblo, 26 Nov.–4 Dec. 1990, 1♀ (A. L. Markezich, MCZ). BRAZIL *Distrito Federal:* km 0 BR 251, 24 Jan. 1990, 1♀ (C. dall'Aglio, MCZ). *São Paulo:* São Paulo, Inst. Botânica, 10 May 1965, 1♀ (P. de Biasi, MZSP). *Rio Grande do Sul:* Barueri, 21, 22 Jan. 1961, 1♂ (MZSP 11522); Garruchos, São Borja, 6 Dec. 1975, 1 imm, 1♀, 1♂; 10 Dec. 1975, 1 imm., 2♂ (A. A. Lise, MCN 3190, 3270, 3265). PARAGUAY *Alto Paraná:* Taquarazapa [? Tacuara], 1♀ (AMNH). ARGENTINA *Santa Fé:* Las Gamas, 20 km W Vera, 25–27 Mar. 1995, 1♀ (M. Ramírez, P. Goloboff, C. Szumik, J. Faivovich, MACN).

Mecynogea buique new species
Figures 55–58; Map 2A

Holotype. Female holotype from between Catimbau and Buíque, Pernambuco, Brazil, 20 Aug. 1982 (P. F. Lins Duarte), in MCN no. 25574. The specific name is a noun in apposition after the locality.

Description. Female holotype. Coloration as in other species, but abdomen with little black pigment dorsally, black pigment only in a pair of posterior black spots in the posterior dark area, other darker areas dorsally lack white pigment (Fig. 58). Total length 7.0 mm. Carapace 2.4 mm long, 1.8 wide in thoracic region, 0.9 wide behind posterior median eyes. First femur 3.3 mm, patella and tibia 3.4, metatarsus 2.9, tarsus 1.1. Second patella and tibia 2.9 mm, third 1.6, fourth 2.5.

Diagnosis. The epigynum of this species (Figs. 55–57) lacks a hood as in females of *M. ocosingo, M. apatzingan* and *M. mar-*

tiana. The epigynum differs from that of *M. ocosingo* in posterior view, having the median plate divided from the laterals by a straight seam (Fig. 56), whereas in *M. ocosingo,* the concave edges of the laterals overlap the median plate (Fig. 60).

Specimens Examined. No other specimens were found.

Mecynogea ocosingo new species
Figures 59–64; Map 2D

Holotype. Male holotype, one male and two female paratypes from Fortin, Veracruz, Mexico, 17 July 1991 (W. H. Piel, G. S. Bodner), in MCZ. The specific name is a noun in apposition after the locality of the first finding of this species.

Description. Female paratype. Coxae yellowish with brown patches. Legs yellowish, venter brown, dorsum of femora with dusky lines. Total length 9.2 mm. Carapace 3.9 mm long, 2.8 wide in thoracic region, 1.3 wide behind posterior median eyes. First femur 5.1 mm, patella and tibia 5.3, metatarsus 4.6, tarsus 1.5. Second patella and tibia 4.8 mm, third 2.7, fourth 4.4.

Male holotype. Total length 7.5 mm. Carapace 3.4 mm long, 2.5 wide in thoracic region, 1.1 wide behind posterior median eyes. First femur 5.0 mm, patella and tibia 5.0, metatarsus 4.9, tarsus 1.6. Second patella and tibia 4.4 mm, third 2.4, fourth 4.0.

Variation. Total length of females 9.0 to 9.3 mm.

Diagnosis. The epigynum of *M. ocosingo* differs from *M. buique* and *M. apatzingan* by having the median lobe emerge from underneath its posterior margin (Figs. 59, 61). The male palpus (Figs. 63, 64) differs from that of *M. apatzingan* by having the two branches of the terminal apophysis of a different shape and slightly smaller.

Natural History. Webs of this large species commonly were found below the webs of *Metepeira incrassata* F. P.-Cambridge (W. Piel, personal communication). One female was collected by beating dead limbs. The spiders have only one large eggsac rather than a string of them as in *M. lemniscata* (C. Hieber, personal communication).

Specimens Examined. MEXICO *San Luis Potosí:* W Xilitla, 10 Aug. 1991, 1♀ (W. H. Piel, G. S. Bodner, MCZ). *Veracruz:* Coscomátepec, 25 Aug. 1963, 1♀ (D. L., H. E. Frizzell, CAS). *Chiapas:* Finca El Real, Ocosingo Valley, 1–7 July 1950, 1♀ (C. and M. Goodnight, L. Stannard, AMNH).

Mecynogea chavona new species
Figures 65, 66; Map 2D

Holotype. Male holotype from Finca Chenevo, 20 km N Río Muco, 20 km S El Porvenir, ca. 170 m, Depto. Meta, Colombia, 1979 (W. Eberhard, no.1391), in MCZ. The specific name is an arbitrary combination of letters.

Description. Male holotype. Carapace orange-yellow without markings. Chelicerae, labium, sternum orange-yellow. Legs orange-yellow, proximal ends of third and fourth coxae brown. Abdomen with usual dorsal pattern; venter with a pair of white lines, each split into three parts. Total length 6.3 mm. Carapace 3.1 mm long, 2.5 wide in thoracic region, 1.1 wide behind posterior median eyes. First femur 4.6 mm, patella and tibia 5.1, metatarsus 4.7, tarsus 1.6. Second patella and tibia 4.2 mm, third 2.5, fourth 4.0.

Diagnosis. The wide proximal branch of the terminal apophysis (Fig. 65) distinguishes the male from that of *M. sucre* (Fig. 38). In both species the tip of the distal branch is covered by the proximal branch.

Specimens Examined. Two imm. from type locality (W. Eberhard, MCZ).

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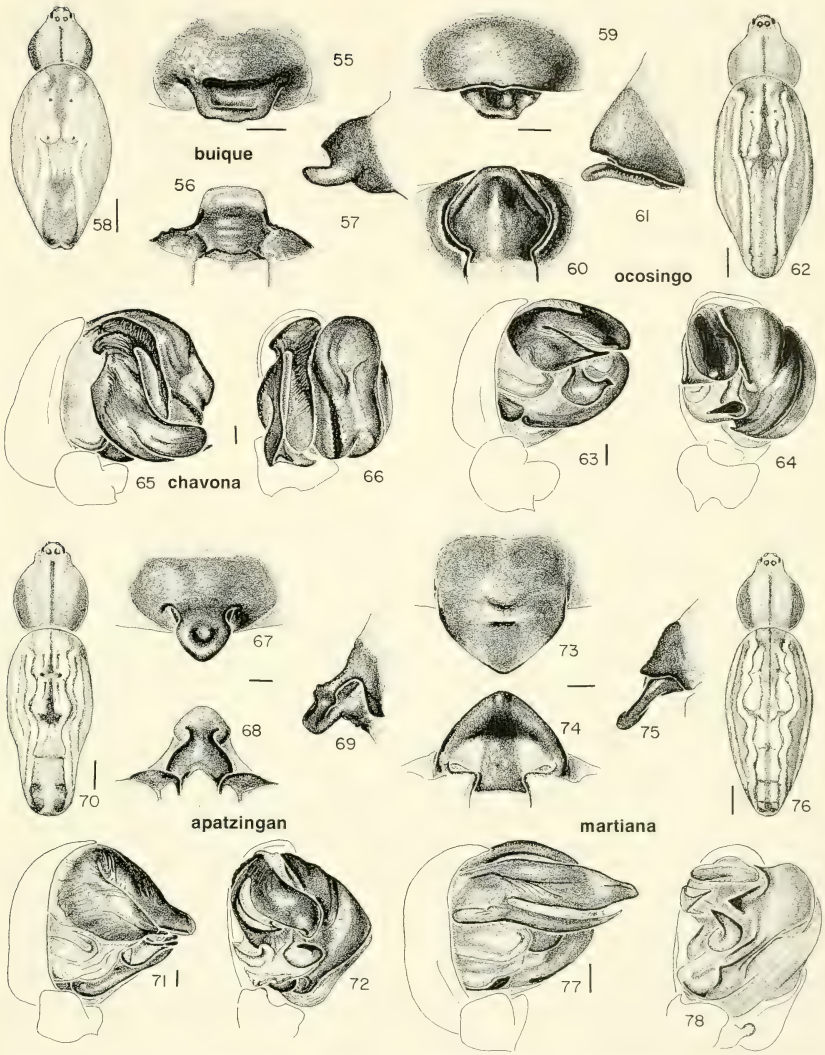
Figures 55–58. *Mecynogea buique* new species, female. 55–57, epigynum. 55, ventral; 56, posterior; 57, lateral. 58, dorsal.

Figures 59–64. *M. ocosingo* new species. 59–62, female. 59–61, epigynum. 59, ventral; 60, posterior; 61, lateral. 62, dorsal. 63, 64, male left palpus. 63, mesal; 64, ventral.

Figures 65, 66. *M. chavona* new species, male palpus. 65, mesal; 66, ventral.



Figures 67–72. *M. apatzingan* new species. 67–70, female. 67–69, epigynum. 67, ventral; 68, posterior; 69, lateral. 70, dorsal. 71, 72, male palpus. 71, mesal; 72, ventral.

Figures 73–78. *M. martiana* (Archer). 73–76, female. 73–75, epigynum. 73, ventral; 74, posterior; 75, lateral. 76, dorsal. 77, 78, male palpus. 77, mesal; 78, ventral.

Scale lines: genitalia 0.1 mm; others 1.0 mm.

Mecynogea apatzingan new species
Figures 67–72; Map 2D

Holotype. Female holotype from Apatzingán, Michoacán, Mexico, 1,200 ft elev. [370 m], July, Aug. 1941 (H. Hoogstraal), in MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Venter of abdomen with long pair of white lines enclosing another shorter pair. Total length 9.6 mm. Carapace 3.5 mm long, 2.8 wide in thoracic region, 1.3 wide behind posterior median eyes. First femur 4.2 mm, patella and tibia 4.6, metatarsus 3.5, tarsus 1.2. Second patella and tibia 4.1 mm, third 2.5, fourth 4.0.

Male from Cocoyoc, Morelos. Coloration as in female. Total length 7.1 mm. Carapace 3.3 mm long, 2.4 wide in thoracic region, 1.2 wide behind posterior median eyes. First femur 4.7 mm, patella and tibia 5.0, metatarsus 4.7, tarsus 1.7. Second patella and tibia 4.5 mm, third 2.4, fourth 4.0.

Note. Males and females were collected together.

Variation. Total length of females 8.2 to 10.1 mm. Some females have the posterior lobe of epigynum with a neck (Fig. 67); others lack the constriction. The illustrations were made from the female holotype and several other specimens, and the male from Cocoyoc, Morelos.

Diagnosis. The epigynum (Fig. 67) resembles that of *Alpaida gallardoi* Levi (Levi, 1988: 431, fig. 300). The equal length and width of the posterior lobe of the epigynum (Fig. 67) and the neck of the median plate in posterior view (Fig. 68) distinguish this species from all other *Mecynogea*. The male is also readily distinguished from other species: in mesal view of the palpus the proximal branch of the terminal apophysis overlaps the length of the distal branch and no space is visible between the branches (Fig. 71).

Natural History. The holotype was taken by sweeping shrubs in semi-desert scrub area.

Specimens Examined. MEXICO *Morelos:* Yautepec, 13 Aug. 1954, 3♀ (R. Dreisbach, MCZ); Cocoyoc, 27 July 1956, 2 imm., 2♀, 2♂ (W. J. Gertsch, V. Roth, AMNH); Cuernavaca, Oct. 1944, 2♀ (N. L. H. Krauss, AMNH); SW Puente de Ixtla, 14 Oct. 1994, 1♀ (W. H. Piel, MCZ). *Puebla:* Acatlán, 24–27 Sept. 1946, 2♀ (H. Wagner, AMNH); 19 km N Acatlán, 3 July 1947, 1♀ (L. I., A. M. Davis, AMNH); Matamoros, 4 Sept. 1945, 1♀ (H. Wagner, AMNH).

Mecynogea martiana (Archer)
Figures 73–78; Map 2D

Allepeira martiana Archer, 1958: 6, figs. 12, 13, 26, ♀, ♂. Male holotype from Carretera Monserrate, Matanzas Prov., Cuba, (P. Alayo), in AMNH, examined.

Mecynogea martiana:—Brignoli, 1983: 274.

Description. Female paratype. Coloration as in other species. Total length 8.8 mm. Carapace 2.8 mm long, 2.4 wide in thoracic region, 1.1 wide behind posterior median eyes. First femur 3.9 mm, patella and tibia 3.8, metatarsus 3.4, tarsus 1.15. Second patella and tibia 3.5 mm, third 1.9, fourth 3.2. All femora slightly longer than patella and tibia of same leg.

Male holotype. Coloration as in female. Total length 5.7 mm. Carapace 2.4 mm long, 2.0 wide in thoracic region, 0.8 wide behind posterior median eyes. Third femur 2.1 mm, fourth 3.4; other leg articles missing.

Diagnosis. The epigynum of *M. martiana* is a triangular sclerite having a shallow, transverse, ventral groove (Fig. 73) unlike that of any other *Mecynogea* species. The male, unlike most other *Mecynogea* species has the distal branch of the terminal apophysis wider than the proximal one (Fig. 77). It differs from *M. bigibba* (Fig. 21) in having the narrow space between the two branches with almost parallel sides (Fig. 77).

Natural History. Both females collected had their webs in agave plants.

Specimens Examined. HAITI Port au Prince, 18–21 July 1955, 4♀ paratypes (A. F. Archer, AMNH). DOMINICAN REPUBLIC Barahona, Sierra Martín García, 8 Aug. 1958, 1♀ (A. F. Archer, E. de Boyroe Moya, AMNH).

Manogea new genus

Type Species. Miranda porracea C. L. Koch, 1839. The name is an arbitrary combination of letters attached to *Gea*. The gender of the name is feminine.

Diagnosis. Manogea differs from all araneids except *Argiope, Gea, Mecynogea, Kapogea* and *Cyrtophora* by having the posterior median eye row straight (*M. porracea* in Fig. 79) or procurved (*M. gaira* and *M. triforma* in Figs. 97, 103). *Manogea* females differ from *Kapogea* and *Cyrtophora* by having a narrow cephalic region (Fig. 79) and slender legs, the first patella and tibia being about 10 times as long as the width of the tibia, whereas in *Kapogea* it is only 6 to 7 times. *Manogea* differs from *Argiope* and *Gea* by having the abdomen tubular to oval, with an anterior pair of tubercles (Figs. 85, 97, 103; 1 in Table 1).

Manogea differs from *Mecynogea* by the pattern on the abdomen: dorsal, straight longitudinal bands that fade anteriorly (Figs. 85, 97, 103). In *Mecynogea* the bands have a wave in the center of the abdomen (Fig. 15). The epigyna in *Manogea* have a pair of openings, each anterior to a cup-shaped structure ([7] in Table 1), sclerotized in *M. porracea* (Figs. 82–84), soft in *M. triforma* and *M. gaira* (Figs. 94, 100). The male palpus lacks the biforked terminal apophysis of *Mecynogea* (Figs. 21, 24); instead there is a distal, soft terminal apophysis (A in Fig. 93), and a small, soft median apophysis (M in Fig. 93).

Description. Females. Coloration (Figs. 85, 97, 103) similar to that of *Mecynogea* (Fig. 15). Anterior median eyes slightly largest, anterior laterals smallest, posterior eyes intermediate (Figs. 79, 88). Eyes of anterior row equally spaced, or median eyes slightly closer to laterals. Posterior eyes equally spaced (Figs. 79, 88). Eye quadrangle wider in front than behind, slightly longer than wide in front (Figs. 79, 80, 87, 88). Clypeus equals about 0.6 diameter of anterior median eyes (Figs. 80, 87). Unlike most other American araneids, but like *Argiope, Mecynogea* and *Kapogea*, all femora are about equal in length to combined patella and tibia of same leg, or the first femur may be slightly shorter. Also, combined metatarsi and tarsi are longer than combined patella and tibia of same leg. In most other araneids, femora are shorter than the patella and tibia, and metatarsi and tarsi are shorter than patella and tibia of the same leg.

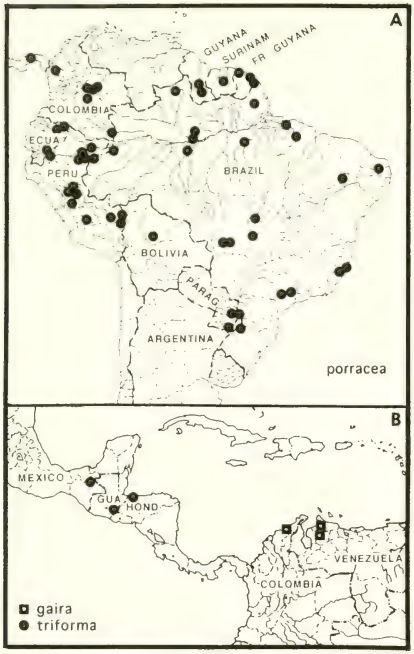
Males. Anterior eyes slightly closer to laterals than to each other (Fig. 88); otherwise similar to females. *Manogea porracea* has a tooth on the endite; other species lack the tooth. All species with one macroseta on palpal patella and two on palpal tibia (Fig. 98). All lack hook on first coxa. Length of males about half to three-quarters that of females.

Genitalia. The epigynum has the paired duct openings anterior to a pair of cup-shaped structures, which are sclerotized, adjacent and posterior in *M. porracea* (Figs. 82–84), soft and lateral in *M. triforma* (Figs. 94–96) and *M. gaira* (Figs. 100–102).

The palpi in all three species are weakly sclerotized. *Manogea porracea* has a weakly sclerotized embolus (E in Fig. 93), a soft median apophysis (M), and a pointed conductor (C) sitting on the tegulum where one might expect a median apophysis. The distal position of the median apophysis resembles that of *Kapogea*. Rarity of male specimens of *M. triforma* and *M. gaira* made study of their palpi difficult. *Manogea gaira* has a long thread-shaped embolus (Figs. 105, 106) that breaks when mating; the distal part remains in the epigynum (Figs. 100, 101). Both *M. gaira* and *M. triforma* have a pointed conductor in the same position as that of *M. porracea*, and a soft median apophysis that extends from behind the radix (Figs. 98, 104).

Silk Glands. Manogea porracea has lost both aggregate and flagelliform silk glands (=*Mecynogea guianensis:*—Kovoor and Lopez, 1988), whereas *Mecynogea* has small aggregate glands.

Relationship. The similarity of *Manogea* to *Mecynogea* and *Kapogea* suggests that



Map 3. Distribution of *Manogea* species.

Manogea occupies an intermediate position.

Natural History. *Manogea porracea* constructs a web similar to those of *Mecynogea* species (Plate 1B).

Distribution. All three species are tropical American.

Separating Species. The species are readily distinguished by the structure of their genitalia.

KEY TO FEMALE *MANOGEA*

1. Epigynum with a pair of sclerotized, adjacent, cup-shaped structures on the posterior margin (Figs. 82–84); Panama to northern Argentina (Map 3A) ..... *porracea*
– Epigynum with cup-shaped structures soft and separated from each other (Figs. 94, 100); southern Mexico to Colombia and Venezuela (Map 3B) 2

2(1). Epigynum a rounded lobe with parallel sides and a cup-shaped structure on each side (Fig. 94); Central America (Map 3B) *triforma*
– Epigynum a median rounded lobe, with pair of shallow notches on each side housing the cup-shaped structures (Fig. 100); northern Colombia and Venezuela (Map 3B) *gaira*

KEY TO MALE *MANOGEA*

1. Embolus flat, wide at base with pointed tip, upper margin almost straight, lower curved, transverse near tip of palpus (Fig. 91, E in Fig. 93); Panama to northern Argentina (Map 3A) ..... *porracea*
– Embolus ribbon-shaped (Figs. 104–106) or not distinct (Figs. 98, 99); Central America, Colombia and Venezuela (Map 3B) 2

2(1). Embolus ribbon-shaped (Figs. 105, 106); northern Colombia and Venezuela (Map 3B) ..... *gaira*
– Embolus hidden and indistinct (Figs. 98, 99); Central America (Map 3B) ..... *triforma*

Manogea porracea (C. L. Koch) new combination

Plate 1B; Figures 79–93; Map 3A

Miranda porracea C. L. Koch, 1839: 49, fig. 368, ♀. Specimen from Brazil, in ZSM, destroyed in the Second World War. First placed in *Cyrtophora* by Simon, 1895a: 773.

Zilla guyanensis Keyserling, 1881: 554, pl. 16, fig. 5, ♂. Two female, two male and an immature syntypes from Cayenne, French Guyana, in PAN, examined. Keyserling, 1893: 301, pl. 15, fig. 222, ♂. Placed in *Cyrtophora* by Levi, 1986: 106. NEW SYNONYMY.

Cyrtophora grammica Simon, 1895b: 156. Female from Tarapoto, Río Mayo, Pebas, Peru, and Le Pará [Belém, Est. Pará], Brazil, in MNHN, examined. Roewer, 1942: 751. Bonnet, 1956: 1366. NEW SYNONYMY.

Zygiella guyanensis:—Roewer, 1942: 887. Bonnet, 1959: 5002.

Cyrtophora porracea:—Roewer, 1942: 751. Bonnet, 1956: 1368.

Mangora albostriata Mello-Leitão, nomen nudum. Determined specimens from Rio Xingú, Pará, Brazil, in MNRJ, examined.

?*Mecynogea carvalhoi* Mello-Leitão, 1944: 8. Female holotype from Barra do Tapirapé [Est. Mato Grosso], Brazil, in MNRJ, lost. Brignoli, 1983: 274. Doubtful. NEW SYNONYMY.

Mangora octolineata Caporiacco, 1947: 25; 1948: 659, fig. 67, ♂. Male holotype from British Guiana [Guyana], in MZUF, examined. Brignoli, 1983: 273. NEW SYNONYMY.

Mecynogea guianensis Mello-Leitão, 1948: 167, fig. 10, ♀. Female from Kutupakari [? Kurupukari],

Essequibo River, Guyana, in BMNH, examined. Brignoli, 1983: 273. NEW SYNONYMY.

Meta brasilica Soares and Camargo, 1948: 380, figs. 37–39, ♀. Female holotype from Chavantina, Mato Grosso, Brazil, in MZSP no. E 777, C 1228, examined. Brignoli, 1983: 230. NEW SYNONYMY.

Meta berlandi Caporiacco, 1954: 80, fig. 14, ♀. Female holotype from Charvein [French Guyana], lost (not in MNHN, MZUF). Brignoli, 1983: 230. NEW SYNONYMY.

Meta espiritosantensis Soares and Camargo, 1955: 578, figs. 4, 5, ♂. Male with both palpi lost from Rio São José, Municipio de Colatina, Est. Espírito Santo, Brazil, in MZSP no. E 458, C 1309, examined. Brignoli, 1983: 230. NEW SYNONYMY.

Mecynogea guianensis:—Levi, 1980: 13; Kovoor and Lopez, 1988.

Cyrtophora guianensis:—Levi, 1991: 179.

Note. Although the illustration lacks the dorsal longitudinal lines on the femora which are present in all *Mecynogea* and *Manogea,* Koch' s illustration and description match this species. Koch's illustration has the cephalic region of the carapace light, framed by dark bands along the lateral cephalic-thoracic depression. Most specimens do not have this coloration, but some specimens from the Amazon area do. Koch's illustration is not a species of *Mecynogea,* because *Mecynogea* are much less common than the species to which the name here is applied; also, all *Mecynogea* species have a median black line on the carapace (it may be indistinct or missing in *M. porracea*).

Keyserling had only a male of *Zilla guyanensis* from Cayenne, but two females, two males and an immature specimen are in the vial. The additional specimens were presumably added later. *Cyrtophora grammica* is an adult female, readily recognized. The specimen of *Mangora albostriata* appears to be a manuscript type, but the description might have been overlooked in an out of the way publication of Mello-Leitão. The holotype of *Mecynogea carvalhoi* is lost, but the size of the specimen described fits this species; also, *Mecynogea* species are much less common than *M. porracea* in the type locality area. The holotype of *Mecynogea guianensis* was examined, and Mello-Leitão provided an adequate silhouette of the epigynum.

The *Mangora octolineata* male holotype was examined; Caporiacco also provided an adequate illustration. The illustration of the epigynum of *Meta berlandi* Caporiacco is recognizable, although the holotype is lost. The *Meta brasilica* holotype was examined and found to be this species. The *Meta espiritosantensis* holotype lost both palpi; however, the markings and shape of the abdomen and illustrations provided are adequate to identify the species.

Description. Female from Brownsberg Reserve, Surinam. Carapace yellow-white with brownish gray sides and narrow median line (Fig. 79). Chelicerae light orange-yellow. Labium, endites brown. Sternum orange with brown rim. Coxae yellow-white, legs yellow-white, with a dorsal, longitudinal brown line on first and second femora; venter of all with dark rings. Abdomen brownish white with white lines and spots (Fig. 85); venter with a pair of white lines, each divided into three, the first the longest, the last a round patch (Fig. 86). Total length 5.2 mm. Carapace 1.9 mm long, 1.5 wide in thoracic region, 0.8 wide behind posterior median eyes. First femur 2.2 mm, patella and tibia 2.3, metatarsus 1.9, tarsus 0.9. Second patella and tibia 2.1 mm, third 1.3, fourth 1.9. First patella and tibia 8.2 times longer than widest region of tibia.

Male from Surinam. Coloration as in female, but dorsal abdominal pattern less distinct (Fig. 90). Tooth on endite. Abdomen as in female but lacks humps (Fig. 90). Total length 3.0 mm. Carapace 1.59 mm long, 1.21 wide in thoracic region, 0.54 wide behind the posterior median eyes. First femur 1.69 mm, patella and tibia 1.74, metatarsus 1.82, tarsus 0.70. Second patella and tibia 1.59 mm, third 0.92, fourth 1.50.

Note. Males and females are commonly collected together.

Variation. Total length of females 4.4 to 9.3 mm, males 2.7 to 4.8. The tip of the embolus (E in Fig. 93) is variable in shape,

sometimes blunt, at other times pointed. Sometimes the posterior eye row is slightly procurved. The illustrations were made from specimens from Brownsberg Reserve, Surinam, but were slightly modified on the basis of specimens from other parts of the range.

Diagnosis. Manogea porracea is readily distinguished from all other American araneids by both the epigynum, with its two dark cup-shaped, adjacent, sclerotized areas on its posterior margin (Fig. 82) and the palpus, with its characteristically shaped embolus and conductor and absence of sclerotized median apophysis (Figs. 91–93). The male, unlike males of other *Manogea* species, has a tooth on the endite. There is no such tooth in *Mecynogea* and *Kapogea* species.

Natural History. Specimens were collected in forested areas in Panama and interior of forests near Manaus, Brazil, and in campo grassland and cerrado shrub in Mato Grosso. The web is illustrated by Plate 1B. Eggsacs have a diamond-shaped outline.

Distribution. Panama to northern Argentina (Map 3A).

Specimens Examined. PANAMA *Panamá:* Pipe Line Road nr. Gamboa (MCZ); Carti Road, 600m (MCZ); Barro Colorado Island (MCZ); Maru Camp, Cerro Azul (MCZ). GUYANA Upper Essequibo River, (AMNH). SURINAM *Brokopondo:* Brownsberg Reserve, 4°50′N, 55°15′W (MCZ). FRENCH GUYANA *Cayenne:* Montagne de Kaw nr. Camp Caïmans, 4°33′N, 52°09′W (USNM); Mont Cabassou nr. Cayenne (MCZ). COLOMBIA *Meta:* Finca Cheveno, 20 km N Río Muco, 20 km S El Porvenir (MCZ); Lomalinda, 3°18′N, 73°22′W (MCZ); Hacienda Mozambique, ca. 15 km W Puerto López (MCZ); 6 km SW Puerto López (MCZ); Río Muco, 20 km N Carimagua (MCZ). *Antióquia:* Mutatá Cancheras (MCZ). *Amazonas:* Río Pira and Apaporis (CAS). ECUADOR *Sucumbíos:* Cuyabeno (MCZ, MECN). *Napo:* Río Coca, Río Napo (MCZ). *Morona-Santiago:* Los Tayos, 1,000 m, 3°06′S, 78°12′W (MCZ). PERU *Loreto:* Explorama Inn, NE Iquitos (FSCA); Campanuto Venodo (MUSM); Cocha Shinguito, 05°08′S, 74°45′W (MUSM); Jénaro Herrera, 04°45′S, 73°45′W (MUSM); Pithecia, 05°11′S, 72°42′W (MUSM); Río Samiria (AMNH). *Amazonas:* Alto Río Comaina, Puesto de Vigilancia (MUSM). *Huánuco:* Monson Valley, Tingo María (CAS); 69 km E Tingo María (CAS); Dantas-La-Molina, SW Puerto Inca, 09°38′S, 75°00′W (MUSM). *Ucayali:* Bosque Nacional A. von Humboldt (MUSM); Panguana, Río Pachitea, 9°37′S, 74°56′W (MCZ). *Pasco:* Huancabamba, 10°10′S, 75°15′W (MUSM). *Madre de Dios:* 15 km E Puerto Maldonado, 12°33′S, 69°03′W (MUSM); Río Tambopata Reserve, 30 km SW Puerto Maldonado (CAS, MCZ); Zona Reservada de Manu, 11°58′S, 71°18′W (USNM); Zona Reservada Pakitza (MUSM). *Ayacucho:* Monterico (PAN). BRAZIL *Amapá:* Serra do Navio (MACN). *Roraima:* Maracá (INPA); Ilha de Maracá, Rio Uraricoera (MCN). *Amazonas:* Manaus (INPA); Ponta Negra, Manaus (MACN); Reserva Ducke, nr. Manaus (INPA, MCN, MCZ); Reserva da Campina, Manaus (MCP); 80 km N Manaus, 2°24′S, 59°52′W (MCZ); Reserv. Colosso (MCZ); Reserv. Km 41 (MCZ); Reserv. Cabo Frio (MCZ); Reserv. Florestal (MCZ); Reserv. Dimona (MCZ); Rio Autaz, Capirauga, Campina Santa Amelia (MRMS); Tabatinga (MCN). *Pará:* Aldeia Arucu, Igarape Gurupi Uma, 50 km E Canindé, Rio Gurupi (AMNH); Canindé, Rio Gurupi (AMNH). *Pernambuco:* Dois Irmãos (MCN). *Paraíba:* Rio Maputro, 16 km S Equador (AMNH). *Espírito Santo:* Reserva Florestal, Linhares (JVN); Rio São José (MZSP). *Mato Grosso:* Poconé (MCP); 260 km N Xavantina, 12°49′S, 51°46′W (MCZ); Chapada dos Guimarães (MCN, MCP); Chavantina (MZSP); Pantal (MCN). *São Paulo:* Botucatu, Vitoviana Carradão (MCZ); Rio Claro (MZSP); Horto Rio Claro (MZSP). *Paraná:* Salto Caxias, Rio Iguaçu (MCN); Fóz do Iguaçú, Refugio Biologico de Bela Vista (MCN); Parque Nacional de Iguaçu (MCN).

→

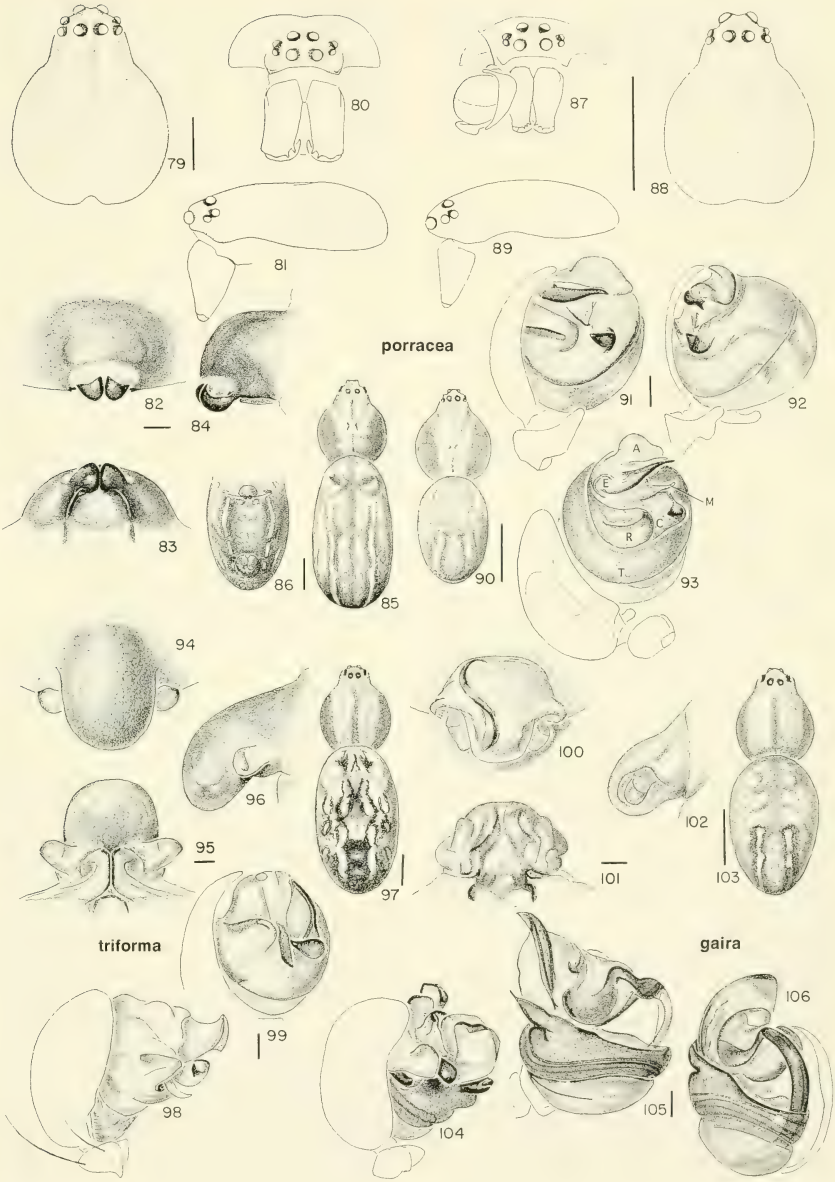
Figures 79–93. *Manogea porracea* (C. L. Koch). 79–86, female. 79, carapace; 80, eye region and chelicerae; 81, carapace and chelicera, lateral. 82–84, epigynum. 82, ventral; 83, posterior; 84, lateral. 85, dorsal; 86, abdomen, ventral. 87–93, male. 87, eye region, chelicerae and right palpus; 88, carapace; 89, carapace and chelicera, lateral; 90, dorsal; 91, left male palpus. 91, mesal; 92, ventral; 93, expanded.

Figures 94–99. *M. triforma* new species. 94–97, female. 94–96, epigynum. 94, ventral; 95, posterior; 96, lateral. 97, dorsal. 98, 99, male palpus. 98, mesal; 99, ventral.

Figures 100–106. *M. gaira* new species. 100–103, female. 100–102, epigynum. 100, ventral; 101, posterior; 102, lateral. 103, dorsal. 104–106, male palpus. 104, mesal; 105, ventral; 106, ectal.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; R, radix; T, tegulum.

Scale lines: genitalia 0.1 mm; others 1.0 mm.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porracea
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triforma
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gaira
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Rio Grande do Sul: Parque de Turvo, Tenente Portela (MCN). BOLIVIA *Beni:* Estación Biológica Beni, 5 km N El Porvenir (USNM). PARAGUAY *Alto Paraná:* Taquarazapa [? Tacuara] (AMNH). ARGENTINA *Misiones:* Parque Nacional Iguazú (MACN); San Ignacio (MLP).

Manogea triforma new species
Figures 94–99; Map 3B

Argiope trivittata:—O. P.-Cambridge, 1889: 51, pl. 4, fig. 6, ♀ [not fig. 5, ♂]. Syntypes from Dolores, Sacrixpur [?], betw. Dolores and Chapallal [?] and San José River near Chiquimuh [Chiquimula, 14°47′N, 89°32′W], Guatemala, in BMNH, examined.

Hentzia trivittata:—F. P.-Cambridge, 1904: 523, pl. 51 [not fig. 12, ♂]. F. P.-Cambridge designated the male as type and females as "gynetypes".

Holotype. Male holotype and female paratype from Palenque Ruins, 17°29′N, 92°01′W, Chiapas, Mexico, 2–11 July 1983 (W. Maddison, R. S. Anderson) in MCZ. The name is an arbitrary combination of letters.

Note. I am following F. P.-Cambridge's type designation and am forced to make a synonym of the name *trivittata* and to name a new species for the female.

Description. Female paratype. Carapace yellowish with three dark longitudinal bands (Fig. 97). Chelicerae yellowish. Labium, endites brown. Sternum yellowish. Legs yellowish with femora having indistinct dorsal lines, other articles with some indistinct black spots. Abdomen white, gray and black (Fig. 97); venter with a pair of white, longitudinal bands, each broken into four elongate patches. Abdomen oval, widest in middle (Fig. 97). Total length 7.2 mm. Carapace 2.9 mm long, 2.2 wide in thoracic region, 1.1 wide behind posterior median eyes. First femur 4.0 mm, patella and tibia 4.0, metatarsus 3.5, tarsus 1.4. Second patella and tibia 3.5 mm, third 2.2, fourth 3.4.

Male holotype. Coloration as in female, but pattern on abdomen less distinct. Height of clypeus equals diameter of anterior median eye. Palpal patella with one macroseta, but two macrosetae on palpal tibia (Fig. 98). Abdomen as in female. Total length 3.7 mm. Carapace 1.85 mm long, 1.45 wide in thoracic region, 0.66 wide behind posterior median eyes. First femur 2.47 mm, patella and tibia 2.60, metatarsus 2.21, tarsus 1.04. Second patella and tibia 2.28 mm, third 1.29, fourth 1.95.

Note. Males and females were collected together.

Variation. Total length of females 7.5 to 14.4 mm. The illustrations were made from specimens from Palenque Ruins, Chiapas, the male palpus from the mirror image of the right palpus.

Diagnosis. The female of this species differs from *M. gaira* by having the median lobe of the epigynum with its sides parallel (Fig. 94), whereas that of *M. gaira* has a shallow notch on each side posteriorly (Fig. 100). The male palpus (Figs. 98, 99) lacks the long coiled embolus of *M. gaira* (Figs. 105, 106).

Natural History. The Chiapas specimens were from the edge of rain forest, the Honduran specimens from beach vegetation.

Specimens Examined. HONDURAS Tela, beach, 26 July 1929, 2♀ (A. M. Chickering, MCZ).

Manogea gaira new species
Figures 100–106; Map 3B

Holotype. Male holotype, six female paratypes from Gaira, 10 m, Depto. Magdalena, Colombia, Dec. 1975 (W. Eberhard), in MCZ. The specific name is a noun in apposition after the locality.

Description. Female paratype. Carapace yellowish with median line and sides of thoracic region gray (Fig. 103). Chelicerae yellow-white. Labium, endites brown. Sternum, legs yellowish. Abdomen dorsum with white patches, large at middle, smaller on sides, and posteriorly with one pair of white bands bordered gray (Fig. 103). Venter with pair of white longitudinal bands, each broken into three pieces and between them some white patches all outlined by gray to black. Total length 3.7 mm. Carapace 1.88 mm long, 1.58 wide in thoracic region, 0.87 wide behind posterior median eyes. First femur 3.02 mm, patella and tibia 2.61, metatarsus 2.01, tarsus 0.90. Second patella and tibia 2.36 mm, third 1.39, fourth 2.05.

Male holotype. Coloration less distinct than that of female. Total length 2.7 mm. Carapace 1.53 mm long, 1.20 wide in thoracic region, 0.53 wide behind posterior median eyes. First femur 1.76 mm, patella and tibia 1.92, metatarsus 1.43, tarsus 0.78. Second patella and tibia 1.69 mm, third 0.94, fourth 1.39.

Note. Males and females were collected together.

Variation. Total length of females 3.7 to 4.2 mm. The illustrations were made from the female paratypes and male holotype.

Diagnosis. The epigynum of the female differs from that of *M. triforma* by having a median bulge with a pair of shallow, lateral notches containing cups with openings (Figs. 100–102). Pieces of broken male embolus show through the transparent bulge (Figs. 100–102). The male differs by having a palpus with a long, coiled, flat embolus (at 3h in Figs. 105, 106).

Paratypes. Nine female paratypes with same data as holotype (Eberhard 1038, EG2 17ff, MCZ).

Specimens Examined. VENEZUELA *Falcón:* Urumaco, 10 July 1972, 1♀, 2 imm. (B. Patterson, MCZ). *Lara:* Quebrada Marín, 5 km NW Altagracia, 2–6 Oct. 1972, 1♀, 6 imm. (B. Patterson, MCZ).

Kapogea new genus

Type Species. Cyrtophora sellata Simon, 1895b. The name is an arbitrary combination of letters attached to *Gea*. The gender of the name is feminine.

Diagnosis. Kapogea differ from most other araneids, except some *Manogea* and *Cyrtophora*, by having the eyes of the posterior eye row straight (Figs. 107, 118) (rarely an individual has the posterior eyes recurved). *Kapogea* females differ from females of *Manogea* by having the cephalic region of the carapace wide (Figs. 107, 129, 136, 144). Also, female *Kapogea* adults are larger than *Manogea* adults, and the legs are thick and relatively short, the total length of the first patella and tibia being about 5 to 7 diameters of the tibia (Fig. 115).

Many *Kapogea* differ from *Cyrtophora* by having two dorsal white lines on the abdomen and by the bodyshape, the elongate, shield-shaped abdomen flattened anteriorly and pointed posteriorly (Figs. 115, 129, 136, 144; [2] in Table 1).

Kapogea always differ from *Cyrtophora* by having two sometimes indistinct openings of the epigynum on a lightly sclerotized hemisphere (Figs. 110, 126, 133, 140; [8] in Table 1), whereas in *Cyrtophora* the openings are anterior to a sclerotized shelf (Figs. 148–150; [9] in Table 1). The palpus of the male is less sclerotized than in *Cyrtophora*. In *Kapogea* the embolus (E) is supported by a flat, soft terminal apophysis (A in Figs. 123–125) with the conductor (C in Figs. 123–125) supporting a soft median apophysis (M), whereas in *Cyrtophora*, the conductor supports the embolus (Figs. 154, 155).

Description. Females. Carapace light to dark without any distinct marks. Abdomen brown, often with a pair of thin, light, longitudinal lines, straight in *K. alayoi* (Fig. 136) and some immature *K. sexnotata* (Fig. 143), jagged in *K. cyrtophoroides* (Fig. 129), and absent in *K. sellata*. Venter with a pair of white lines on black, and a white patch on each side of spinnerets (Fig. 116). Anterior eyes equally spaced, or medians farther from laterals. Posterior median eyes closer to each other than to laterals (Figs. 107, 108). Lateral eyes separated by 0.7 to 1.2 diameters of posterior lateral eye (Fig. 108). Ocular quadrangle wider in front than behind, longer than wide in front (Figs. 107, 108). Height of clypeus less than diameter of anterior median eye (Fig. 108). Third and fourth femora about equal in length to combined patella and tibia of same leg. Length of metatarsus and tarsus about equal in length to patella and tibia of same leg (Fig. 115). Legs thick (Fig. 115), length of first patella and tibia about 6 to 7 times width of tibia.

Males. Less than 20 percent of total length of female (left in Figs. 115, 129, 136, 144). Coloration as in female. Cephalic region about half width of thoracic region, sometimes wider or narrower (Fig. 118). Anterior eyes equally spaced or medians closer to laterals (Figs. 117, 118)

than to each other. Spacing of posterior row of eyes variable. Lateral eyes barely separated (Fig. 118). Third and fourth femur almost as long, equal in length or slightly longer than combined patella and tibia of same leg; metatarsus and tarsus of equal length. Legs thick. Endite without tooth, palpal patella with one seta, first coxa without hook. Shape of abdomen oval (Figs. 120, 132, 139, 147).

Silk Glands. The aggregate and flagelliform silk glands are assumed to be absent (judging by their absence in both *Manogea* and *Cyrtophora*), but no specimens have been examined.

Relationship. The many similar characters place *Kapogea* close to *Cyrtophora.* The support of the palpal median apophysis by the conductor is specialized in *Kapogea.*

Natural History. The webs observed are similar to the webs of *Mecynogea* species, horizontal and lacking viscid threads (Plates 2A, B, C).

Distribution. All four species are tropical American.

Separating Species. Females can be distinguished by the shape and coloration of the abdomen (Figs. 115, 129, 136, 144). The epigyna of all are quite similar, that of *K. sellata* (Fig. 110) being most distinct. The males also are easiest to distinguish by the coloration of the abdomen (Figs. 120, 132, 139), except for *M. sexnotata* (Fig. 147) which has a distinct palpus (Figs. 145, 146). But perhaps mistakes were made with separating the males: *Kapogea sellata* had 17 collections of females, five of males; *K. cyrtophoroides* 24 and 10; *K. alayoi* 22 and three; *K. sexnotata* 22 and four.

Illustrations of the dorsal side of the epigynum were made one for each species, and almost no differences were found between species. (Perhaps, if an illustration for each specimen were made, distinguishing characters might be discovered.) Illustrations of terminal apophysis of the palpus were made in dorsal view; individual variation was found, but no useful differences between species. Neither set of illustrations is reproduced here.

KEY TO FEMALE *KAPOGEA*

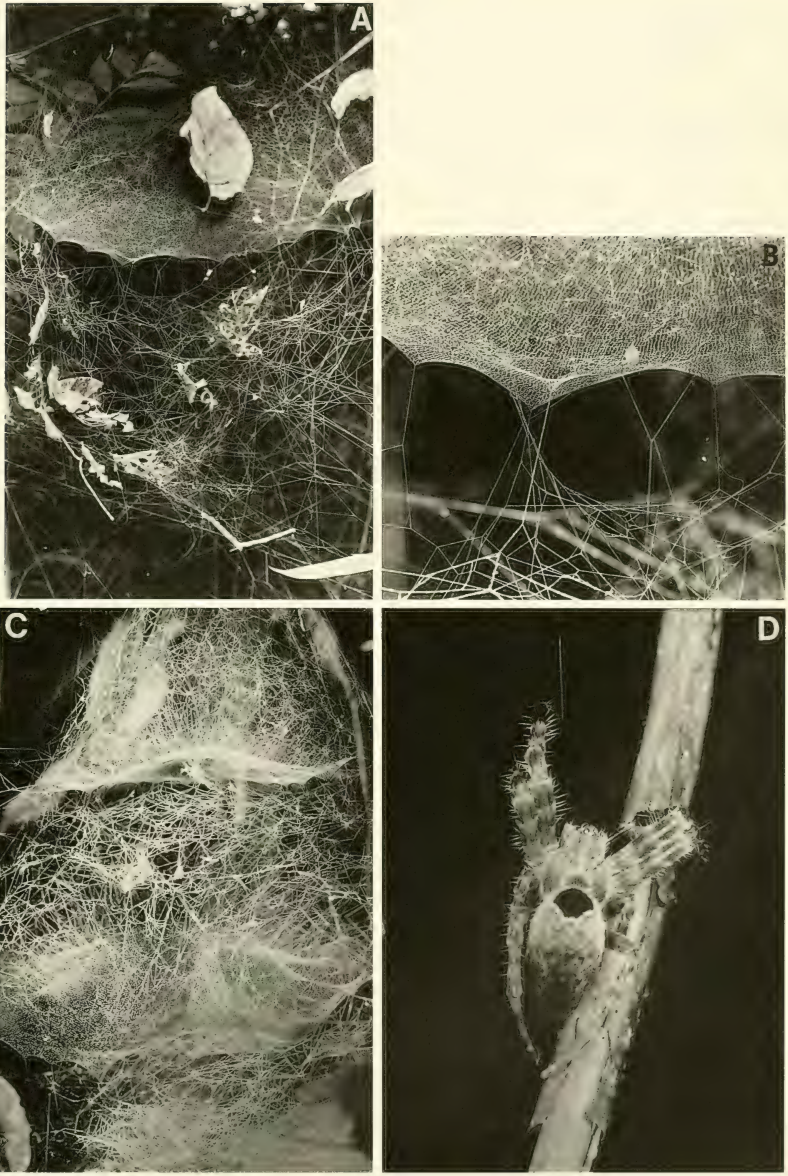
1. Abdomen with a distinct, well defined, black patch anteriorly between humps (Fig. 115); Greater Antilles, Costa Rica to Argentina (Map 4A) ..... *sellata*
– Abdomen otherwise (Figs. 129, 136, 144) 2
2(1). Adult abdomen black with three pairs of white spots (Fig. 144); adult total length more than 17.5 mm; Venezuela and upper Amazon area (Map 4D) ..... *sexnotata*
– Abdomen with a pair of lines, rarely brown without marks (Figs. 129, 136); adult total length usually less than 17 mm 3
3(2). Abdomen with zigzag lines, humps located dorsally (Fig. 129); southern Mexico to Amazon region (Map 4C) ..... *cyrtophoroides*
– Abdomen with straight lines and dorsal or projecting lateral humps (Figs. 136, 143) 4
4(3). Abdomen with humps laterally (Fig. 136); Bahamas, Greater Antilles, Panama to northern Argentina (Map 4B) ..... *alayoi*
– Abdomen of immature with humps dorsally (Fig. 143) ..... *sexnotata*

KEY TO MALE *KAPOGEA*

1. Palpus with median apophysis distally biforked into two short filaments (between center and 3h in Fig. 145, center in Fig. 146) and terminal apophysis with lip (at 12h in Fig. 145); Venezuela, upper Amazon area (Map 4D) ..... *sexnotata*
– Palpus with median apophysis not biforked, having only one short filament, terminal apophysis without lip (M in Fig. 124, and in Figs. 121, 130, 137) 2
2(1). Abdomen with lobed folium pattern (Fig. 132), southern Mexico to Amazon region (Map 4C) ..... *cyrtophoroides*
– Abdomen marked otherwise (Figs. 120, 139) 3
3(2). Abdomen with anterior black patch (Fig. 120); Greater Antilles, Costa Rica to Argentina (Map 4A) ..... *sellata*

→

Plate 2. A, web of *Kapogea sellata* in Panama. B, detail of web. C, webs of *K. alayoi* in Peru, width of photo is 12 cm. D, female *K. sellata* from Peru, laboratory photo. (Photos A, B, Y. Lubin; C, J. Coddington)


A
B
C
D

– Abdomen with two almost straight white lines and lateral, anterior humps (Fig. 139); Bahamas, Greater Antilles, Panama to northern Argentina (Map 4B) ..... *alayoi*

Kapogea sellata (Simon) new combination

Plate 2; Figures 107–122; Map 4A

Cyrtophora (Evatria) sellata Simon, 1895b: 155. One female holotype from Santo Domingo Isl. [presumably Hispaniola], in MNHN, examined.

Araneus rugosus Franganillo, 1936: 75, fig. 33, tarsal tip. Specimen from Habana Prov., Cuba, in ACCH, examined. Name preoccupied by Badcock, 1932: 24. NEW SYNONYMY.

C. sellata:—Roewer, 1942: 751. Bonnet, 1956: 1368. Blanke, 1976: 125, fig. 1, ♀.

Note. A labeled specimen of *Araneus rugosus* from ACCH was examined.

The male illustrated by Blanke (1976), collected in Vitoria, Est. Espírito Santo, Brazil, with a female, is apparently the male of *K. sexnotata*. The specimen is lost.

Description. Female from near Putumayo, Colombia. Carapace golden-yellow with some white setae (Fig. 115). Chelicerae dark brown. Labium, endites lighter brown. Sternum brown. Coxae lighter brown than sternum. Legs yellow-brown, first and second tibia with dark distal ring. Third and fourth with brown ring, more distinct on venter. Abdomen light brown, darkest posteriorly with an anterior, almost circular, median brown patch framed by a light line (Fig. 115), sides of abdomen much lighter, venter with a pair of white brackets, facing each other (Fig. 116). Carapace with a shallow transverse thoracic depression. Anterior median eyes 0.9 diameter apart, 1.8 diameters from laterals. Posterior median eyes 1.0 diameter apart, 2.5 diameters from laterals. Lateral eyes separated by 0.5 diameter of posterior lateral. Total length 18 mm. Carapace 7.0 mm long, 4.9 wide in thoracic region, 3.0 wide in cephalic region. First femur 6.5 mm, patella and tibia 7.1, metatarsus 4.7, tarsus 1.7. Second patella and tibia 6.7 mm, third 3.8, fourth 5.8.

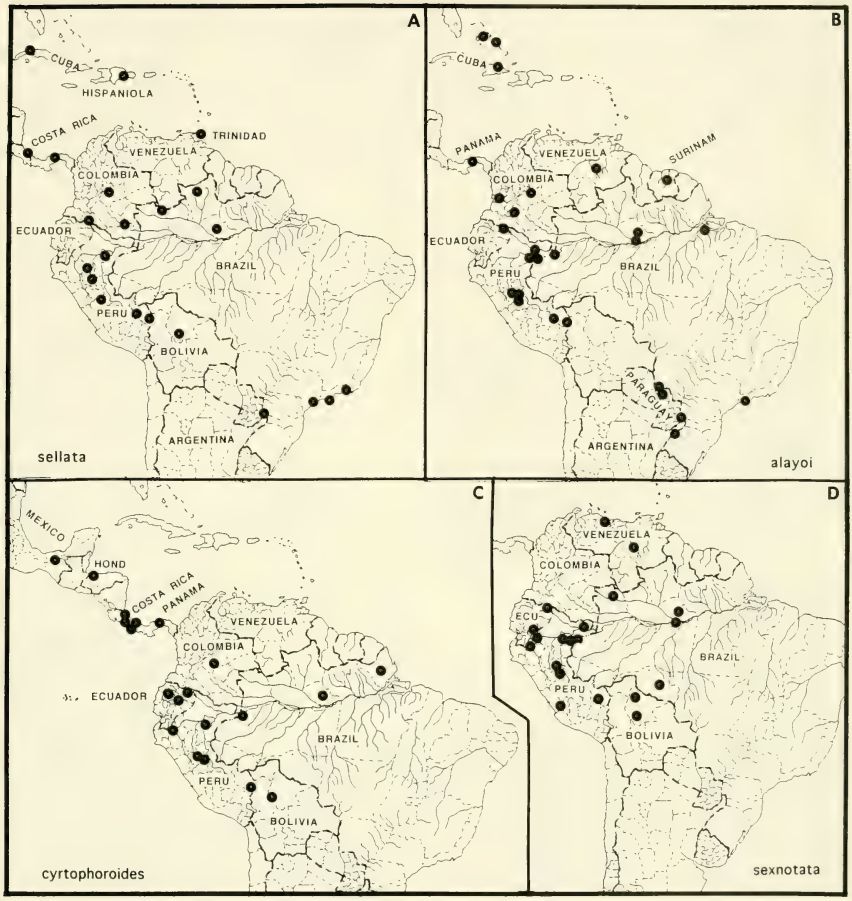
Male from near Moyobamba, Peru. Carapace dark brown, yellowish between eyes, with a pair of elongate lighter patches behind eyes (Fig. 120). Chelicerae orange-brown, with a dark patch. Labium, endites light brown. Sternum brown. Legs with first coxae and femora dark, others light; distal end of tibia with wide brown rings. Abdomen whitish with anterior median black patch (Fig. 120), as in female; venter with white spots and gray pigment. Anterior median eyes 0.7 diameter apart, 0.3 diameter from anterior laterals. Posterior median eyes 1.0 diameter apart, 0.9 diameter from posterior laterals. Laterals separated by 0.5 diameter of posterior lateral eye. Total length 2.7 mm. Carapace 1.56 mm long, 1.14 wide in thoracic region, 0.62 wide behind posterior median eyes. First femur 1.63 mm, patella and tibia 1.78, metatarsus 1.17, tarsus 0.65. Second patella and tibia 1.62 mm, third 0.79, fourth 1.23.

Note. Males and females can be paired on the basis of the similar dark patch on the abdomen, but have not been collected together.

Variation. Total length of females 12.2 to 19 mm, males 2.7 to 2.8. The eye sizes of the male described (Fig. 120) and the one illustrated differ slightly (Figs. 117–119). The illustrations were made of a female from Colombia; Figures 117–119 from a male from Colombia; Figures 120–122 from a male from Peru. Some males lack the dark patch on the abdomen and are difficult to determine.

Diagnosis. The dark patch on the anterior of the abdomen in males and females facilitates ready distinction from other *Cyrtophora* species. (The venter of the epigynum has a pair of round to oval openings with transparent frame, difficult to see, and difficult to compare with other species.) The longest lobe of the terminal apophysis of the male palpus seems narrower and longer (Fig. 121) than that of other species.

Natural History. Specimens have been collected at the forest edge in the Dominican Republic, in humid forest in Costa Rica, in forest in Panama and in forest in-



Map 4. Distribution of *Kapogea* species.

terior at Reserva Dimona, Manaus, Brazil (Plate 2).

Distribution. Greater Antilles, Costa Rica to Argentina (Map 4A).

Specimens Examined. GREATER ANTILLES *Dominican Republic. Sánchez-Ramírez:* Mina Pueblo Viejo nr. Hatillo, 500m, 21 Mar. 1984, 4 imm.,1♀ (H., L. Levi, MCZ). LESSER ANTILLES *Trinidad:* St. Augustine, Nov. 1944, 1♀ (R. H. Montgomery, AMNH).

COSTA RICA *Limón:* Penshurst, 10 km N Cahuita, 13–15 Apr. 1983, 1 imm. (D. Ubick, DU). PANAMA *Panamá:* Barro Colorado Island, 29 July 1939, 1 imm. (A. M. Chickering, MCZ); 30 Aug. 1969, 1 imm.; 14 Sept. 1973, 1♀; 18 Nov. 1973, 1♀ (both Y. Lubin, MCZ); Pipeline Road, 19 July 1976, 1♀ (M. Robinson, MCZ).

COLOMBIA *Meta:* Hacienda Mozambique, 15 km

SW Puerto López, June 1978, 1♂ (W. Eberhard, MCZ). *Putumayo:* Río Putumayo nr. Puerto Asis, no date, 1♀ (W. Eberhard, MCZ). *Amazonas:* Araracuaro, 270 m, 10 Mar. 1988, 1♀ (C. Valderrama, CV). PERU *Loreto:* Alto Río Samiria, 10 May 1950, 1♀ (D. Silva, MUSM). *Pasco:* Huancabamba, Quebrada Castillo, NW Iscozacin, 10°10′S, 75°15′, 6 Sept. 1987, 1♂ (D. Silva, MUSM). *San Martin:* Mishiqui-yacu, 20 km NE Moyobamba, Aug. 1947, 1♂ (F. Woytkowski, AMNH); Juanjui, 350 m, 16–24 Aug. 1948, 1♀ (D. Silva, MUSM). *Madre de Dios:* Tambopata Reserve, Río Tambopata, 30 Mar. 1988, 1♀ (J. Palmer, D. Smith, MCZ); 2 May 1988, 1♀ (D. Silva, MUSM); Zona Reservata Pakitza, 9–13 May 1991, 2♀ (D. Silva, MUSM). BRAZIL *Roraima:* Estação Ecológica de Maracá, Ilha de Maracá, Rio Uraricoera, 21–30 Nov. 1987, 1♂ (J. A. Rafael, MCN 23349). *Amazonas:* Parque Nacional do Pico da Neblina, 28 Sept. 1990, 1♀ (A. A. Lise, MCP); Reserva Dimona, 80 km N Manaus, 26 Mar. 1991, 1♀ (H. Fowler, R. S. Vieira, E. Venticinque, MCZ). *Rio de Janeiro:* Pinheiro, Rio de Janeiro, 1 imm. (MNRJ). *São Paulo:* Poco Grande, Juquiá, Jan. 1898, 2♀ (E. Simon determ., MZSP 8037); Ilha de São Sebastião, 1♀ (Lange, MNRJ). BOLIVIA *Beni:* 27 km SW Yocomo, 15°23′S, 66°59′W, 15–19 Nov. 1989, 1♂ (J. Coddington et al., USNM). ARGENTINA *Misiones:* Par. Nacional Iguazú, Oct. 1979, 1♀ (M. E. Galiano, MACN); 24–30 July 1992, 1♀ (M. J. Ramírez, MACN).

Kapogea cyrtophoroides (F. O. P. Cambridge)
new combination
Figures 123–131; Map 4C

Araneus cyrtophoroides F. O. P.-Cambridge, 1904: 518, pl. 51, fig. 4, ♀. Female holotype from Teapa [Est. Tabasco], Mexico, in BMNH, examined. Bonnet, 1955: 481.

Araneus setospinosus Chamberlin and Ivie, 1936: 48, pl. 14, fig. 124, ♀. Female holotype from Barro Colorado Island [Lago Gatún, Panamá Prov.], Panama, in AMNH, examined. Bonnet, 1955: 598. NEW SYNONYMY.

Cyrtophora nympha:—Levi (1991: 178). Not *C. nympha* Simon.

Aranea cyrtophoroides:—Roewer, 1942: 840.

Aranea setospinosa:—Roewer, 1942: 852.

Note. The holotype of *Araneus cyrtophoroides* is the most northern specimen of this species collected. *Araneus setospinosus* types were examined and the description has good illustrations to synonymize the name. The synonymy of *A. cyrtophoroides* and *A. setospinosus* in Levi (1991: 178) is in error.

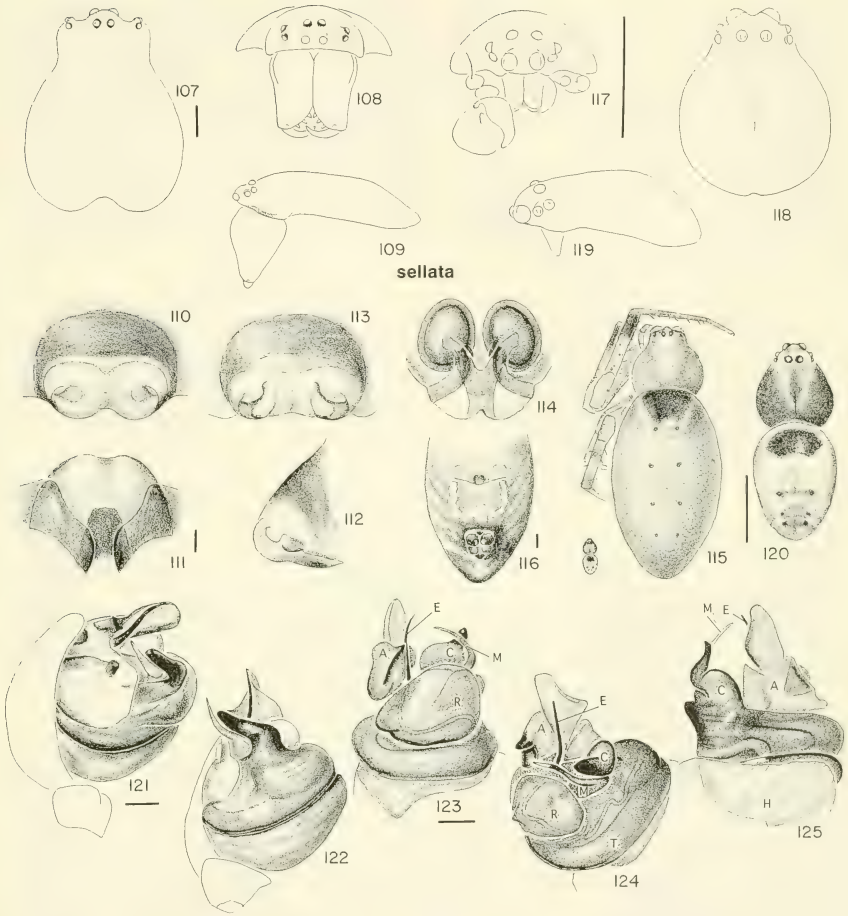
Description. Female from La Selva, Costa Rica. Carapace light orange-brown (Fig. 129). Chelicerae, labium, endites, sternum light dusky orange-brown. Coxae, legs light orange-brown without rings. Abdomen light orange-brown with a pair of zigzag, longitudinal white lines. Anterior ends of lines originating on hump and bordered by black hairs (Fig. 129); venter of abdomen with two white brackets on black, no white spots on sides of spinnerets. Anterior median eyes 1.2 diameters apart, 1.2 diameters from laterals. Posterior median eyes 1.2 diameters apart, 2.2 diameters from laterals. Lateral eyes separated by diameter of posterior laterals. Total length 10.5 mm. Carapace 5.4 mm long, 4.1 wide in thoracic region, 2.3 wide in cephalic region. First femur 4.7 mm, patella and tibia 5.2, metatarsus 3.0, tarsus 1.4. Second patella and tibia 4.8 mm, third 3.0, fourth 4.5.

Male from Costa Rica. Carapace dark brown. Chelicerae yellowish with gray streaks. Labium and endites brown to dark brown. Sternum yellowish. Legs with wide brown rings, first two femora brown. Abdomen black, with a pair of jagged lines dorsally (Fig. 132) and a pair of broken white lines ventrally. Total length 2.7 mm. Carapace 1.33 mm long, 1.11 wide in thoracic region, 0.57 wide in cephalic region. First femur 1.13 mm, patella and tibia 1.29, metatarsus 0.78, tarsus 0.51. Second patella and tibia 1.17 mm, third 0.65, fourth 0.97.

Note. Males and females were matched because they were both collected at La Selva, Costa Rica; Lomalinda, Colombia; and on Barro Colorado Island and have similar abdominal color pattern.

Variation. Total length of mature females 7.2 to 13.5mm, males 2.5 to 2.7. Rarely, the abdomen lacks folium pattern, making determination difficult.

Diagnosis. The abdomen is oval in both sexes, with the humps dorsal (Figs. 129, 132), unlike that of *K. alayoi* (Figs. 136, 139) which has the humps lateral. *Kapogea cyrtophoroides* has a pair of zigzag white lines on each side dorsally (Figs. 129, 132),



Figures 107–122. *Kapogea sellata* (Simon). 107–116, female. 107, carapace; 108, eye region and chelicerae; 109, carapace and chelicera, lateral. 110–114, epigynum. 110, 113, ventral; 111, posterior; 112, lateral. 110–112, (from Depto. Meta, Colombia); 113, (from São Paulo, Brazil). 114, cleared, dorsal; 115, dorsal with male on left. 116, abdomen, venter 117–122, male. 117, eye region chelicerae and right palpus; 118, carapace; 119, carapace and chelicera, lateral; 120, dorsal. 121, 122, left male palpus. 121, mesal; 122, ventral.

Figures 123–125. *K. cyrtophoroides* (F. P.-Cambridge), male left palpus, expanded. 123, subdorsal; 124, submesal; 125, subventral.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; H, hematodocha; M, median apophysis; R, radix; T, tegulum.

Scale lines: genitalia 0.1 mm; others 1.0 mm.

whereas *K. alayoi* has a pair of nearly straight, dorsal white lines (Figs. 136, 139).

Natural History. Specimens were found by shaking foliage in wet tropical forest in Costa Rica, in forest in southern Peru.

Distribution. Southern Mexico to Amazon Region (Map 2C).

Specimens Examined. HONDURAS Lancetilla nr. Tela, mountain trail, 22 July 1929, 1♀ (A. M. Chickering, MCZ). COSTA RICA *Heredia:* La Selva nr. Puerto Viejo, 15–27 Sept. 1981, 1♂; Oct. 1981, 2 imm. (C. E. Griswold, CAS); Feb. 1981, 1♀, 1♂ (W. E. Eberhard, ♂ 2201, MCZ); May 1986, 1♂ (W. Eberhard, 3272, MCZ). *San José:* Quizarra, 6 km E San Isidro, May 1989, 1♂ (W. Eberhard, MCZ); 3 km NE Golfito, 22–23 May 1987, 1♂ (D. Ubick, DU). PANAMA *Bocas del Toro:* Bocas del Toro, 15 Sept. 1975, 1♀ (E. de Fuentes, MIUP). *Panamá:* Barro Colorado Island, Mar. 1933, 1♀ (F. Lutz, AMNH); June 1936, 1♂ (A. M. Chickering, MCZ); Madden Dam area, 2 Sept. 1956, 1♀ (W. Lundy, AMNH); Pipeline Road, 19 Mar. 1976, 1♀; Jan., Feb. 1977, 1♂ (M. Robinson, ♂ raised from egg, MCZ); Gamboa, Pipeline Road, Aug., Sept. 1976, 1♀ (M. Robinson, MCZ).

COLOMBIA *Meta:* Lomalinda, Puerto Lleras, 3°18′N, 73°22′W, Mar. 1980, 6♂; 12 July 1985, 1♀; 12 Dec. 1985, 1♀ (W. T. Carroll, MCZ); Mar.–Apr. 1986, 2♂ (V., B. Roth, W. T. Carroll, CAS). ECUADOR *Pichincha:* Tinalandia, 12 km E Santo Domingo de los Colorados, 11–17 May 1986, 1♀ (G. B. Edwards, FSCA). *Sucumbíos:* Reserva Faunistica Cuyabeno, Laguna Grande, 0°00′, 76°10′W, 5 Aug. 1988, 1♀, determ. uncertain (W. Maddison, 88–021, MCZ); Limoncocha, 300 m, 24–26 June 1980, 1♀ (H. V., C. B. Weems, FSCA). *Pastaza:* Puyo, Río Pastaza, 14 Apr. 1958, 1♀ (W. Weyrauch, CAS). PERU *Loreto:* Alto Río Samiria, 05°07′S, 75°28′W, 1♀ (D. Silva, MUSM); Cocha Shanguito, 05°08′S, 74°45′W, 25 May 1990, 2♀ (D. Silva, MUSM). *Amazonas:* Alto Río Comaina, Puesto de Vigilancia Falso Paquisha, 21 Oct.–3 Nov. 1987, 2 imm., 2♀ (D. Silva, MUSM). *Huánuco:* 69 km E Tingo María, 5 Oct. 1954, 1 imm. (E. S. Ross, E. I. Schlinger, CAS); Monson Valley, Tingo María, 19 Oct. 1964, 1♀ (E. I. Schlinger, E. S. Ross, CAS); Dantas la Molina, SW de Puerto Inca, 18 May–1 June 1987, 1♀ (D. Silva, MUSM). *Madre de Dios:* 15 km E Puerto Maldonado, 200 m, 12°33′S, 69°00′W, 22 June–16 July 1989, 3 imm., 1♀ (D. Silva, MUSM); Zona Reservata Tambopata, 290 m, 31 July 1987, 1♀; 20 Sept. 1991, 1♀ (D. Silva, MUSM). BRAZIL *Amapá:* Serra do Navio, June 1966, 1♀ (M. E. Galiano, MACN). *Roraima:* Ilha de Maracá, Rio Uraricoera, 17 July 1987, 1♀ (A. A. Lise, MCN 20063). *Amazonas:* Tabatinga, Aug. 1984, 1♀ (A. Cerrutti, MNRJ); Reserva Cabo Frio, 21 Sept. 1989, 1♀ (H. Fowler, R. S. Vieira, E. Venticinque, MCZ). BOLIVIA *Beni:* 19.5 km S Rurrenabaque, 14°38′S, 67°20′W, 22 Nov. 1989, 1♂ (J. Coddington et al., USNM).

Kapogea alayoi (Archer) new combination
Figures 133–139; Map 4B

Cyrtophora alayoi Archer, 1958: 9, figs. 14–16, ♂. Male holotype from Banes, Oriente Prov. [now in Holguin Prov.], Cuba, in AMNH, examined. Brignoli, 1983: 267.

Note. The holotype of the name *Cyrtophora nympha* has straight, dorsal, abdominal lines (Fig. 143), and I considered the name once as a senior synonym of both *K. cyrtophoroides* and *K. alayoi,* before I had distinguished the last two species. But the holotype of *C. nympha* is an immature as are all the specimens closest to the *C. nympha* type, all of larger size than mature *C. cyrtophoroides* and *C. alayoi,* and all are believed to be immatures of *C. sexnotata.*

Description. Female from Pipeline Road [Prov. Panamá], Panama. Carapace light brown, with white and brown setae (Fig. 136). Chelicerae labium, endites, brown. Sternum brown. Legs brown. Abdomen with a pair of straight white lines dorsally (Fig. 136); venter with a white, L-shaped band on spider's right, facing a

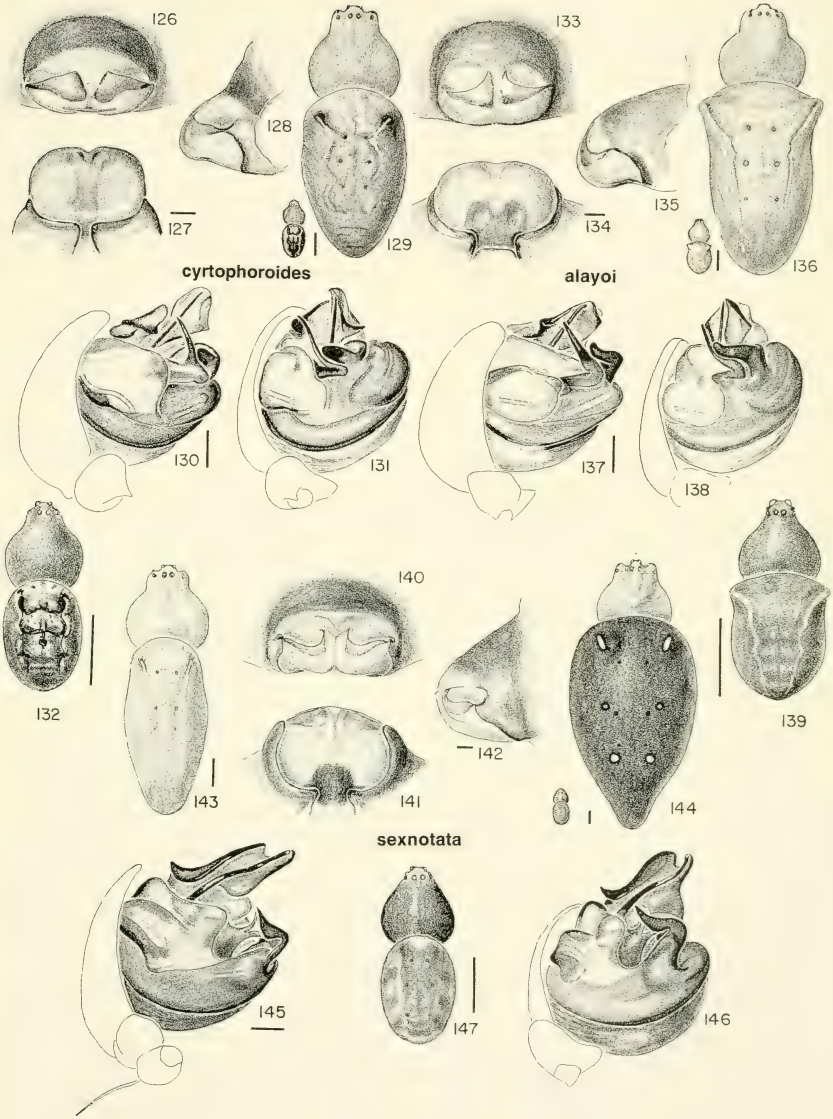
→

Figures 126–132. *Kapogea cyrtophoroides* (F. P.-Cambridge). 126–129, female. 126–128, epigynum. 126, ventral; 127, posterior; 128, lateral. 129, dorsal with male on left. 130–132, male. 130, 131, left male palpus. 130, mesal; 131, ventral. 132, dorsal.

Figures 133–139. *Kapogea alayoi* (Archer). 133–136, female. 133–135, epigynum. 133, ventral; 134, posterior; 135, lateral. 136, dorsal with male on left. 137–139, male. 137, 138, male palpus. 137, mesal; 138, ventral. 139, dorsal.

Figures 140–147. *Kapogea sexnotata* (Simon) 140–144, female. 140–142, epigynum. 140, ventral; 141, posterior; 142, lateral. 143, immature, dorsal; 144, dorsal with male on left. 145–147, male. 145, 146, male palpus. 145, mesal; 146, ventral. 147, dorsal.

Scale lines: genitalia 0.1 mm; others 1.0 mm.


126
127
128
129
cyrtophoroides
133
134
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136
alayoi
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143
139
144
sexnotata
145
147
146

similar band on left, both on black; otherwise venter brown, spinnerets dark brown. Anterior median eyes 1.1 diameters apart, 1.1 diameters from laterals. Posterior median eyes 1.1 diameters apart, two diameters from laterals. Laterals separated by the diameter of posterior lateral eye. Total length 12 mm. Carapace 5.0 mm long, 4.3 wide in thoracic region, 2.1 wide behind posterior median eyes. First femur 5.1 mm, patella and tibia 5.6, metatarsus 4.1, tarsus 1.4. Second patella and tibia 5.1 mm, third 2.9, fourth 4.4.

Male holotype. Coloration as in female (Fig. 139), but legs with first femur and tibia brown, others ringed brown on yellowish. Anterior median eyes 0.9 diameter apart, 0.4 diameter from laterals. Posterior median eyes 0.8 diameter apart, 0.9 diameter from laterals. Lateral eyes separated by 0.5 diameter of posterior lateral. Posterior eye row slightly recurved. Total length 2.6 mm. Carapace 1.27 mm long, 1.05 wide in thoracic region, 0.58 wide behind posterior median eyes. First femur 1.09 mm, patella and tibia 1.25, metatarsus 0.74, tarsus 0.48. Second patella and tibia 1.09 mm, third 0.60, fourth 0.83.

Note. Males and females were matched because both have the same shape, the abdomen with anterior, lateral humps, and have straight lines on the dorsal surface of the abdomen.

Variation. Total length of females 9.5 to 14.5 mm. The illustrations were made from a female from Pipeline Road, Panama, and the male holotype from Cuba.

Diagnosis. In both females and males *Kapogea alayoi* differs from *K. cyrtophoroides* by having a shield-shaped abdomen with lateral, pointed humps (Figs. 136, 139), whereas that of *K. cyrtophoroides* is oval with dorsal humps (Figs. 129, 132). The abdomen has two almost straight lines, whereas (Figs. 129, 132) that of *K. cyrtophoroides* has a folium bordered by a jagged line on each side (Figs.129, 132).

Natural History. "I was struck by the similarity to the webs of *Mecynogea* and *Cyrtophora,* both of which I have seen. But in this spider the orb (which has the fine, dry mesh with divergent radii) is not dome-shaped but rather is flatter and somewhat turned up at the rim. It has the extensive irregular webbing above and below to which the horizontal catching web is attached by guy lines as in the other two genera. The hub is closed and egg sacs are suspended separately and scattered about in the meshwork under the orb. The spider stays in a retreat in a patch of debris suspended in the irregular webbing just under the rim of the orb. It is nocturnal and rests in the hub only at night. Usually the web site is in dense brush about 1.5 m above the ground." [From letter by J. Carico (1992) about the female collected on the Bahama Islands.]

Distribution. Bahamas, Greater Antilles, Panama to northern Argentina (Map 4B).

Specimens Examined. BAHAMA ISLANDS Waterloo, Nassau, Mar. 1913, 2♀ (C. J. Maynard, J. E. Thayer, MCZ); San Salvador, 28 Dec 1991–4 Jan. 1992, 1♀ (J. Carico, MCZ).

PANAMA *Panama:* Pipeline Road, Gamboa, Aug., Sept. 1976, 1♀; Jan.–Feb. 1977, 1♀, 1♂ (M. Robinson, MCZ).

VENEZUELA *Bolívar:* Río Caura, Campamento Cecilia Magdalena, 7 May 1957, 1♀ (D. Rabayna, CAS). SURINAM *Brokopondo:* Brownsberg Reserve, 4°50′N, 55°15′W, May 1984, 1♀ (D. Smith, MCZ). COLOMBIA *Meta:* 6 km SW Puerto López, 1978, 1♀ (W. Eberhard 1487, MCZ). *Valle:* Cali, 1,000 m, 17 Oct. 1967, 1 imm. (W. Eberhard 45B, MCZ); June 1975, 1♀ (W. Eberhard, MCZ); 1976, 1♀ (W. Eberhard, MCZ). *Caqueta:* Río Orteguaza, 200 m, Aug., Sept. 1947, 1♀ (L. Richter, AMNH). ECUADOR *Sucumbíos:* Río Tarapoy, 20 Feb. 1989, 1 imm. (L. Avilés, MECN). PERU *Loreto:* Génaro Herrera, 100 m, 04°45′S, 73°45′W, 25 Aug. 1988, 1♀ (S. Silva, MUSM); Explorama Inn, 40 km NE Iquitos, 19–21 July 1989, 1♀ (H. V. Weems, FSCA); Pithecia, 5°11′S, 72°42′W, 16 Aug. 1989, 1♀ (D. Silva, MUSM); 27 May 1990, 1♀ (D. Silva, MUSM). *Huánuco:* Dantas la Molina, SW Puerto Inca, 270 m, 09°38′S, 75°00′W, 18 May–1 June 1987, 1♀ (D. Silva, MUSM); Monson Valley, Tingo María, 23 Sept.–10 Oct.1954, 1 imm., 1♀ (E. I Schlinger, E. S. Ross, CAS). *Pasco:* Huancabamba, Quebrada Castillo, NW Iscozacin, 10°10′S, 75°15′W, 6–9 Sept. 1983, 5 imm. (D. Silva, MUSM). *Madre de Dios:* Zona Reservada Pakitza, 6 Oct. 1987, 1♀ (J. Coddington, D. Silva, MUSM); Zona Reservada Manu, 5 km upstream from Pakitza, 11°58′S, 71°18′W, 4 Oct. 1987, 1 imm. (D. Silva, J. Coddington, USNM); Pueste de Vigil Pakitza, 11°58′S, 71°18′W, 4–6 Oct. 1987, 1 imm., 1♀ (D. Silva, J. Cod-

dington, USNM); Zona Reservada Tambopata, 290 m, 15 May 1988, 1♀ (D. Silva, MUSM). BRAZIL *Pará:* Caixuana, Melgaço, 15 Aug. 1996, 1♀ (A. A. Lise, MCP). *Amazonas:* Benjamin Constant, Sept. 1962, 1♀ (K. Lemke, MZSP 9541); Reserva do Km 41, 80 km N Manaus, 26 Feb. 1989, 1♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ); Fazenda Esteio, 80 km N Manaus, 13 Jan. 1994, 1♀ (A. D. Brescovit, MCN 25362); Reserva Ducke, Manaus, 18–25 Feb. 1992, 1♀ (A. D. Brescovit, MCN 22033). *São Paulo:* Caraguatatuba, 10–16 July 1965, 1 imm. (Exped. Depto. Zool., MZSP 4934). *Rio Grande do Sul:* Garruchos, São Borja, 10 Nov. 1979, 1♂ (A. A. Lise, MCN 8673); Santa Maria, São Marcos, 24 Nov. 1995, 1♂ (C. Kotzian, L. Indrusiah, MCP). PARAGUAY *Concepción:* Apa, Aug. 1909, 1♀ (? E. Reimoser, AMNH); S. Louis [San Luis de la Sierra, 22°25′S, 57°27′W, R. Paynter and M. Caperton, 1977], Oct. 1908, 1♂ (? E. Reimoser, AMNH). ARGENTINA *Misiones:* Parque Nacional Iguazú, July 1985, 2 imm. (M. Ramírez, MACN).

Kapogea sexnotata (Simon) new combination
Figures 140–147; Map 4D

Cyrtophora sexnotata Simon, 1895b: 155. Female holotype from Tefé [Amazonas State], Brazil and Iquitos, Peru, in the MNHN, examined. Roewer, 1942: 751. Bonnet, 1956: 1368.

C. nympha Simon, 1895b: 156. Immature female holotype from San Esteban, Venezuela, in MNHN, examined. Roewer, 1942: 751. Bonnet, 1956: 1367. NEW SYNONYMY.

?*C. sellata*:—Blanke, 1976: 125, fig. 2, ♂ (not female).

Note. The male collected with a female of *K. sellata* in Vitoria, Espírito Santo, Brazil (Blanke, 1976) is *K. sexpunctata.*

Description. Female from 80 km N Manaus. Carapace orange-brown, darkest between eyes, but lightest between and posterior to anterior median eyes (Fig. 144). Chelicerae orange-brown, darkest distally. Labium, endites, sternum orange-brown with indistinct lighter patches. Legs orange-brown with indistinct lighter rings. Abdomen black with three pairs of white spots dorsally, first pair a streak, second and third pairs round, second pair smallest (Fig. 144). Anterior median eyes one diameter apart, 2.4 diameters from laterals. Posterior median eyes 1.5 diameters apart, 2.5 diameters from laterals. Laterals separated by diameter of posterior lateral eye. Total length 23 mm. Carapace 8.4 mm long, 6.2 wide in thoracic region, 3.5 wide in cephalic region. First femur 7.7 mm, patella and tibia 8.8, metatarsus 6.2, tarsus 2.3. Second patella and tibia 8.5 mm, third 5.2, fourth 7.0.

Male from 80 km N of Manaus. Carapace dark brown with area between eyes yellowish; a dark band between anterior eyes running to each posterior median eye. Chelicerae yellow-white with dark patch. Labium, endites brown and orange-brown. Sternum yellowish white with brown on sides, diffusing toward center. First coxae dark, others light. Legs yellowish white but with first femur dark brown, distal end of tibia with wide ring. Abdomen dorsally gray, lighter anteriorly with a pair of indistinct white lines; sides with broad dark bands narrowing ventrally and toward the posterior (Fig. 147). Venter gray with a pair of white brackets. Anterior median eyes 0.9 diameter apart, 0.7 diameter from anterior laterals. Posterior median eyes 0.9 diameter apart, 0.8 diameter from posterior laterals. Laterals separated by one-third the diameter of posterior lateral eye. Sternum with pair of slight transverse swellings anteriorly and in center with a small seta on pointed tubercle. Total length 3.2 mm. Carapace 1.57 mm long, 1.24 wide in thoracic region, 0.71 wide in cephalic region. First femur 1.44 mm, patella and tibia 1.55, metatarsus 1.00, tarsus 0.55. Second patella and tibia 1.43 mm, third 0.78, fourth 1.17.

Note. Males and females were matched because they were collected in abundance on the reservations 80 km north of Manaus, Brazil.

Variation. Total length of females 17.5 to 25 mm, males 2.8 to 3.3. Immature females and some adults have a pair of dorsal lines (Fig. 143) resembling *K. alayoi* (Fig. 136) but lack the anterior, lateral abdominal humps. Other immatures are patterned as in the adult. The illustrations were made from females and males from near Manaus, Brazil.

Diagnosis. The dorsal markings of the abdomen, three pairs of white spots on

black (Fig. 144), are diagnostic and distinguish this species from others. Some immatures have two white lines (Fig. 143) resembling *K. alayoi*, but have dorsal humps and may be larger than adult *K. alayoi*. The male can be distinguished from the other *Kapogea* species by its median apophysis, which has a pair of short filiform projections (between center and 3h in Fig. 145, center in Fig. 146); other species have only one such projection (M in Fig. 124, Figs. 121, 130, 137). Unfortunately, the median apophysis is soft, small and not easily examined. The long lobe of the terminal apophysis, unlike that of other species, has a lip distally from the palpus (at 12h in Fig. 145).

Natural History. The spider collected at Los Tayos, Ecuador, was on a single dead leaf, in a three-dimensional web, without obvious orb, and 1.5 m across in several directions.

Distribution. Venezuela, upper Amazon area (Map 4D).

Specimens Examined. VENEZUELA *Bolívar:* Río Caura, Campamento Cecilia Magdalena, 7 May 1957, 1 imm. (D. Robayna, CAS). ECUADOR *Sucumbíos:* Reserva Faunistica Cuyabeno, Laguna Grande, Sendero, 0°00′, 76°10′W, 26 June 1988, 1♀ (W. Maddison, 88–006, MCZ), 1 Apr. 1994, 1 imm. (G. Estévez, MECN). *Morona-Santiago:* Los Tayos, 3°06′S, 78°12′W, 29 July 1976, 1 imm. (MCZ). PERU *Loreto:* Tipishca del Río Samiria, 8 May 1990, 1♀ (D. Silva, MUSM); Génaro Herrera, 04°45′S, 73°45′W, 23–28 June 1988, 4♀ (D. Silva, MUSM); Pithecia, 05°11′S, 72°42′W, 14 Aug. 1989, 1♀ (D. Silva, MUSM); Estirón, Río Ampiyacu, 13 Nov. 1961, 1♀ (B. Malkin, AMNH); Río Bombo, Alto Tapiche [04°59′S, 73°51′W, Stephens and Traylor, 1983], Jan. 1928, 1♀ (H. Bassler, AMNH). *Amazonas:* Alto Río Comaina, Puesto de Vigilancia Falso Paquisha, 21 Oct–3 Nov. 1987, 1♀ (D. Silva, MUSM). *Cajamarca:* Río Chinchipe nr. San Ignacio, 1,200 m, July 1948, 1♀ (W. Weyrauch, CAS). *Ucayali:* Divisoria, 1,700 m, 23 Sept.–3 Oct. 1946, 1 imm. (F. Woykowski, AMNH). *Huánuco:* Dantas La Molina, Quebrada Sapote, SW Puerto Inca, 09°38′S, 75°00′W, 18 May–1 June 1987, 1♀ (D. Silva, MUSM). [? *Lima*]: Aquaitia [? Aquicha], 1, 2 Sept. 1946, 33♀ (F. Woytowski, AMNH). *Madre de Dios:* Zona Reservada Pakitza, 13 Oct. 1991, 1♀ (D. Silva, MUSM). BRAZIL *Amazonas:* Rio Negro Umarituba, 16 Apr. 1924, 1♀ (A. Roman, NRMS); Manaus, Reserva Ducke, 25 Aug. 1977, 1♀ (Y. Lubin, MCZ); 80 km N Manaus, 2°24′S, 59°52′W, 1989, 1♀; 17 Jan. 1989, 1♂; 26 Feb. 1989, 1 imm.; 9 Mar. 1989, 1♂; 11 June 1989, 1 imm.; 8 July 1989, 1♂; 22 Aug. 1989, 1 imm.; 8 Sept. 1989, 1♀ (all H. G. Fowler, MCZ); Reserva Cabo Frio, 80 km N Manaus, 9 Apr. 1989, 1♀ (H. Fowler, R. S. Vieira, E. Venticinque, MCZ); Reserva Colosso, 24 Nov. 1988, 1♀; 10 Nov. 1988, 4 imm., 3♀ (H. G. Fowler, MCZ); 18 Jan. 1989, 1 imm., 1♀; 8 July 1989, 1 imm, 1♀ (H. Fowler, R. S. Vieira, E. Venticinque, MCZ); Reserva Dimona, 80 km N Manaus, 1889–1992, 3 imm. (H. G. Fowler, MCZ); 27 Mar. 1991, 1♀ (H. Fowler, R. S. Vieira, E. Venticinque, MCZ); Reserva Porto Alegre, 80 km N Manaus, 1989–1992, 1♀ (H. G. Fowler (MCZ). *Rondônia:* Fazenda Rancho Grande, NE Cacaulandia, 6–15 Dec. 1990, 1 imm. (J. E. Eger, FSCA). BOLIVIA *Beni:* Chacobo Indian Village, 12°30′S, 66°W, July, Aug. 1960, 3♀ (B. Malkin, AMNH); Est. Biol. Beni, 225 m, 14°47′S, 66°15′W, 8–14 Nov. 1989, 1♂ (J. Coddington et al., USNM).

Cyrtophora Simon

Cyrtophora Simon, 1864: 262. Type species *C. citricola* designated by Simon, 1895a: 775. Neave, 1939a: 951. The gender of the name is feminine (Bonnet, 1956: 1360).

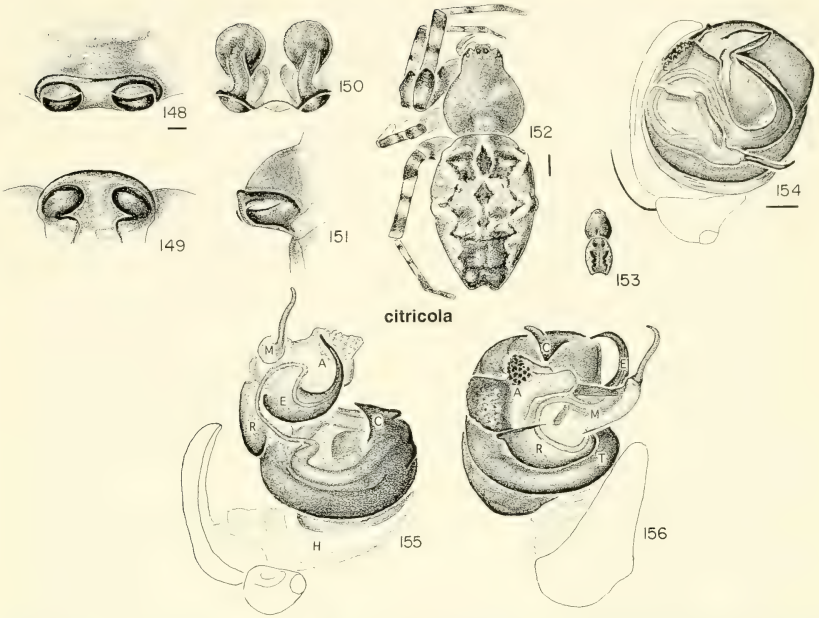
Euetria Thorell, 1890: 109. Type species *C. molluccensis*. Neave, 1939b: 323. Simon (1895a: 771) synonymized *Evetria* [sic] with *Cyrtophora*.

Evetria:—Simon, 1893: 322. An invalid "correction" of Thorell's spelling of *Euetria*. The name *Evetria* is preoccupied by Huebner, 1825 (as cited in Neave, 1939b: 386).

Diagnosis. Cyrtophora differs from other araneids (except *Argiope, Gea, Mecynogea, Manogea* and *Kapogea*) by the proportions of the leg articles, having the second to fourth combined patella and tibia slightly shorter than the femur of the same leg and also shorter than the combined metatarsus and tarsus of the same leg. Additional characters are the relatively heavy legs, and the slight separation of the lateral eyes.

Cyrtophora differs from *Argiope, Gea* and *Mecynogea* by having the posterior eye row recurved or straight. It differs from *Manogea* by having a wide cephalic region of the carapace.

Cyrtophora differs from *Kapogea* by having the posterior eye row usually recurved (Fig. 152), the openings of the epigynum sclerotized (Figs. 148–151; [9] in Table 1), the embolus (E) of the palpus placed near the median apophysis (Fig. 154, M in Fig. 156), and the embolus supported by the conductor (Fig. 154, C in



Figures 148–156. *Cyrtophora citricola* (Forskål). 148–152, female. 148–151, epigynum. 148, ventral; 149, posterior; 150, dorsal, cleared; 151, lateral. 152, dorsal. 153–156, male. 153, dorsal. 154–156, left male palpus. 154, mesal; 155, expanded, submesal. 156, expanded, dorsal.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; H, hematodocha; M, median apophysis; R, radix; T, tegulum.

Scale lines: genitalia 0.1 mm; others 1.0 mm.

Map 5. Distribution of *Cyrtophora citricola* in America.

Fig. 155). Also the abdomen may have more than one pair of humps and may be posteriorly biforked (Fig. 152; [3] in Table 1).

As in *Kapogea*, but unlike *Mecynogea* and *Manogea*, the males are dwarfed and the females large (Figs. 152, 153).

Natural History. The orb web of *Cyrtophora* is horizontal, has a very fine mesh and lacks viscous threads. It has been described for a number of species.

Australians and South Africans refer to the *Cyrtophora* species as tent spiders (Lubin, personal communication).

Distribution. Cyrtophora has many species world-wide in warmer areas; only one

is introduced in America. The species from Africa are least known.

Misplaced Species. Argiope marxi McCook, 1894: 223, is *Cyrtophora moluccensis* (synonymized by Levi, 1968: 334) with an erronous G. Marx locality.

Cyrtophora californensis Keyserling, 1885, is a *Eustala* (Levi, 1977: 104).

C. davisi (Hingston, 1932; Levi, 1991: 179) is a *Spilasma* (Levi, 1995: 187).

C. lodiculafaciens (Hingston, 1932: 365) is not a *Cyrtophora* (Levi, 1995: 209). The web is horizontal but not *Cyrtophora*-like (Hingston, 1932: figs. 45, 46). It is a *Dolichognatha* according to W. Eberhard (personal communication).

C. vachoni Caporiacco, 1954: 82 is an immature *Azilia* (Tetragnathidae). NEW COMBINATION.

Cyrtophora citricola (Forskål) Figures 148–156; Map 5

Aranea citricola Forskål, 1775: 86.
Cyrtophora citricola:—Simon, 1864: 262. Roewer, 1942: 747. Bonnet, 1956: 1362.

Description. Both sexes with posterior eye row strongly recurved (Figs. 152–153). Lateral eyes separated by diameter of posterior lateral eyes. Total length of female about 10.3 mm, male about 3.1. Palpus of male without patellar setae, but two long setae on palpal tibia. Endite without tooth. Conductor attached to outer edge of tegulum (Figs. 155, 156).

Distribution. Mediterranean, Africa, southern Asia, recently found introduced in southern Colombia.

Natural History. The spider is abundant in ornamental trees, wild trees and fruit trees. The fine, strong web tangles up the branches of trees until these die through asphyxiation. Within the web we have observed both nocturnal and diurnal insects, as well as harmful and beneficial ones. From the nearby highway it is possible to see many trees completely dried up and dead, tangled up in the web (letter from N. C. Mesa C., Aug. 1996, Palmira, Colombia).

Records. COLOMBIA *Valle:* Cauca Valley, July 1996, 4♀ (H. Kuratomi, MCZ).

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New Species of Lizards, Genus *Stenocercus* (Iguania: Tropiduridae), from Western Ecuador and Peru

JOHN E. CADLE

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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NEW SPECIES OF LIZARDS, GENUS *STENOCERCUS* (IGUANIA: TROPIDURIDAE), FROM WESTERN ECUADOR AND PERU

JOHN E. CADLE[1]

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ABSTRACT. Three new species of *Stenocercus* (Iguania: Tropiduridae) are described from northwestern Peru and southwestern Ecuador. *Stenocercus limitaris* new species is known from localities in El Oro and Loja provinces, Ecuador, and Tumbes and Piura departments, Peru. It is similar to species of *Ophryoessoides sensu* Fritts in having large posterior head scales and supraoculars and keeled ventrals. *Stenocercus latebrosus* new species is known from southern Cajamarca and western La Libertad departments, Peru, and is characterized by a pair of well-developed mite pockets on each side of the neck underneath the antehumeral and oblique neck folds. Such pockets are found elsewhere in *Stenocercus* only in *S. ornatissimus* and in some populations referred to *S. chrysopygus*. *Stenocercus stigmosus*, new species, is known from central Cajamarca department, Peru. Males of *S. stigmosus* have bold black spots covering the entire venter. Description of these species resulted in a revised conception of *Stenocercus ornatissimus* (Girard), for which a lectotype is designated and brief notes are provided. It is definitely known only from Lima department, Peru. However, some populations in Ancash department (Peru) presently referred to *S. chrysopygus* may not be distinguishable from *S. ornatissimus*. In addition, some problems concerning geographic variation and the status of various populations referred to *S. chrysopygus* are outlined.

RESUMEN. Se describen tres nuevas especies de *Stenocercus* (Iguania: Tropiduridae) del noroeste del Perú y el suroeste del Ecuador. *Stenocercus limitaris* nueva especie se conoce de localidades en las provincias El Oro y Loja, Ecuador, y los departamentos Tumbes y Piura, Perú. Esta especie es similar a especies de *Ophryoessoides* según Fritts al tener grandes escamas en la parte posterior de la cabeza, grandes supraoculares, y ventrales quilladas. *Stenocercus latebrosus* nueva especie se conoce del departamento Cajamarca septentrional y del departamento La Libertad occidental, Perú. Se caracteriza por un par de bolsillos acáridos bien desarollados en cado lado del cuello debajo de los pliegues antehumerales y obliquos. Se encuentran tal bolsillos entre otras especies de *Stenocercus* solamente en *S. ornatissimus* y en algunas poblaciones atribuidas a *S. chrysopygus*. *Stenocercus stigmosus* nueva especie se conoce de la parte central del departamento de Cajamarca, Perú. En los machos de *S. stigmosus* manchas pronunciadas negras cubren todo el vientre. Las descripciones de estas especies resultaron en una idea revisada de *Stenocercus ornatissimus* (Girard), de la cual se escogió un lectotipo y se provee de notas breves. Definitivamente esta especie se conoce solamente en el departamento de Lima, Perú. Sin embargo, algunas poblaciones en el departamento de Ancash (Perú) que se refieren actualmente a *S. chrysopygus* no sean bien distinguidas de *S. ornatissimus*. Además, se resumen algunos problemas acerca de la variación geográfica y el estado de varias poblaciones atribuidas a *S. chrysopygus*.

[1] Museum of Comparative Zoology, 26 Oxford Street, Harvard University, Cambridge, Massachusetts 02138.

INTRODUCTION

This paper is part of an ongoing series to help clarify the systematic status and biogeography of herpetofaunal components of the Andes and adjacent areas of northwestern Peru and southern Ecuador. Previous papers described new species of snakes (Cadle, 1989), frogs (Cadle and McDiarmid, 1990) and lizards (Cadle, 1991; Cadle and Chuna, 1995) from the area. Clearly, the diversity of amphibians and reptiles in the area is significantly underestimated at present. Including the new species cited above, more than 18 new species have been described from the Cordillera Occidental of northwestern Peru and southern Ecuador in the last nine years (references cited above; Duellman, 1991;[2] Duellman and Wild, 1993; Orcés and Almendáriz, 1989; Wiens, 1993).

Similarly, the species diversity of many Andean genera of amphibians and reptiles is poorly known. One example is the lizard genus *Stenocercus* (Iguania: Tropiduridae), which is widely distributed in South America from the high Andes to the lowlands on either side. Although Cadle (1991) described five new species of *Stenocercus* from northern Peru, he pointed out that many new species of *Stenocercus* were known from existing collections and merely awaited description and that new species continued to be discovered at a high rate. This paper describes three new species from the western Andean slopes and western interandean valleys (Amazonian slopes) of northern Peru and southern Ecuador.

[2] Duellman (1991) described *Eleutherodactylus petrobardus* (Anura: Leptodactylidae) and stated that it inhabited the Pacific slopes of the Andes. However, the type (and only known) locality is east of the continental divide in the interandean valley of the Ro Chotano, and is thus Amazonian (not Pacific). The stated longitude of 76°57'W (Duellman 1991: 6) seems to be a lapsus for 78°57'W, given the other stated type locality information.

MATERIALS AND METHODS

All species described herein are assigned to *Stenocercus* Duméril and Bibron *sensu lato* (including *Ophryoessoides* Duméril), for reasons discussed by Frost (1992) and Cadle (1991). General descriptive protocols follow Cadle (1991), who gave definitions of *Stenocercus* scale, neck fold, and mite pocket terminology based in part on Frost (1992). Colors were recorded in the field in life and supplemented with color slides. Bilateral scale counts (e.g., subdigitals) were done only on one side (the left, unless it was damaged), except for holotypes, for which both left and right counts are listed (l–r). A summary of selected scutellational and qualitative characters for the new species and two previously described species emphasized herein are presented in Table 1.

All measurements are in millimeters. The abbreviation SVL refers to the head–body length, snout to vent. The configuration of neck folds and mite pockets vary considerably among species of *Stenocercus* and are useful in distinguishing species. The most important qualitative characteristics of these features used herein are the following, which are discussed more fully by Cadle (1991).

Neck Folds. Antehumeral fold—a more or less vertical fold immediately anterior to the forelimb insertion. Oblique fold—a neck fold more or less parallel to the antehumeral fold located laterally on the neck about midway between the forelimb insertion and the posterior border of the ear.

Posthumeral (Axillary) and Postfemoral Mite Pockets. Type 1—pocket absent; no skin modification. Type 2—rudimentary pocket manifested by skin modification, such as bare skin or a series of wrinkles, or a shallow depression lined with scales different from surrounding body scales. Type 3—similar to Type 2, but with an overhanging fold of skin or a thickened border. Type 4—a deep pocket, usually with a broad circular opening, whose

TABLE 1. SELECTED MERISTIC, MENSURAL, AND QUALITATIVE CHARACTERISTICS OF THE NEW SPECIES OF *STENOCERCUS* DESCRIBED HEREIN AND OF *S. ORNATISSIMUS* (GIRARD) AND *S. CHRYSOPYGUS* BOULENGER. QUANTITATIVE CHARACTERS ARE GIVEN AS RANGE FOLLOWED BY MEAN ± 1 SD (MODE RATHER THAN MEAN GIVEN FOR SOME CHARACTERS). SAMPLE SIZES (*N*) ARE GIVEN AT THE TOP OF EACH COLUMN EXCEPT WHERE THEY VARIED FOR INDIVIDUAL MEASURES (*N* ADDED PARENTHETICALLY).

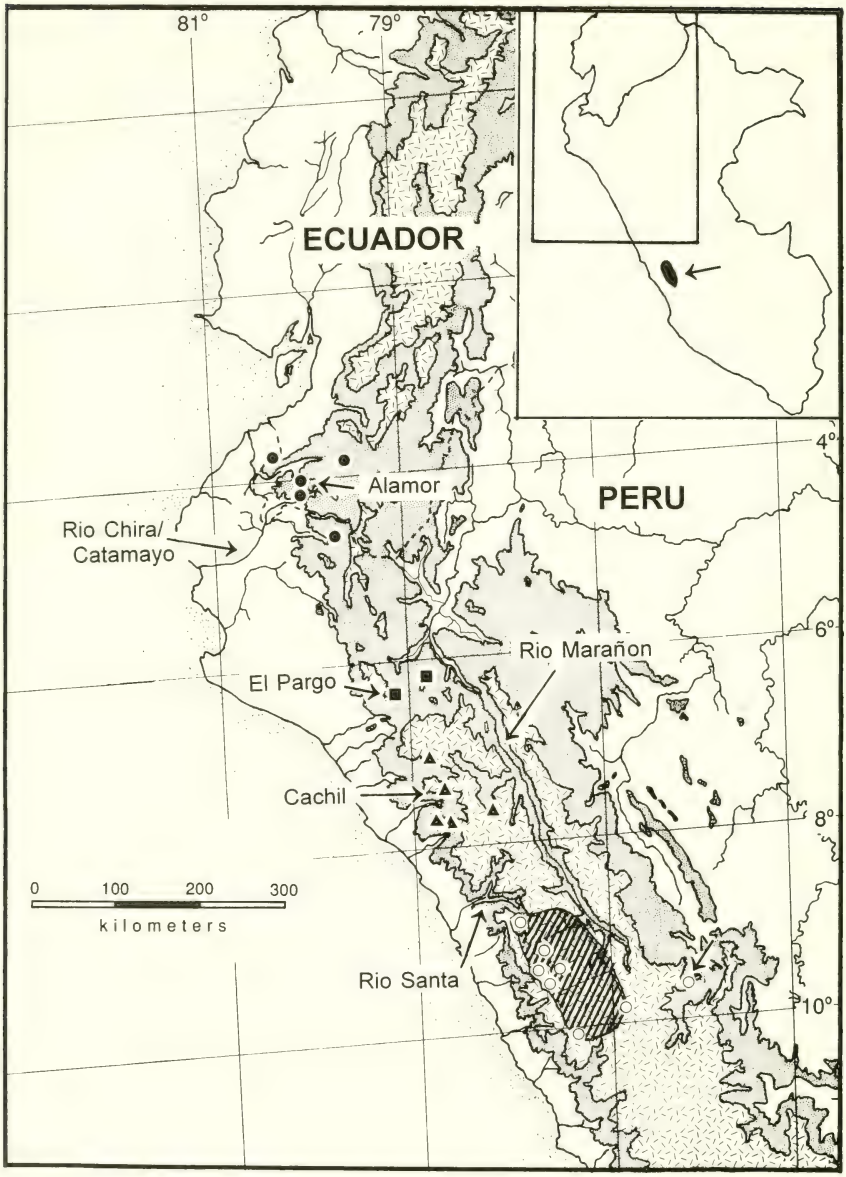
	Stenocercus limitaris new species *N* = 44	*Stenocercus latebrosus* new species *N* = 37	*Stenocercus stigmosus* new species *N* = 12	*Stenocercus ornatissimus* (Girard, 1857) *N* = 21	*Stenocercus chrysopygus* Boulenger, 1900[1] *N* = 22
Midbody scales	39–54 47.3 ± 3.16 (*N* = 43)	38–57 44.2 ± 4.19	49–57 52.7 ± 2.27	49–60 52.6 ± 3.03 (*N* = 18)	43–67 52.1 ± 6.67 (*N* = 19)
Vertebral scales	40–52 45.7 ± 2.54 (*N* = 43)	43–53 48.2 ± 3.07 (*N* = 36)	51–61 56.4 ±3.09	52–59 55.4 ± 2.38 (*N* = 18)	50–73 57.2 ± 6.25 (*N* = 19)
Gular scales	17–23 20.1 ± 1.28 (*N* = 43)	18–26 20.9 ± 1.79	19–27 23.3 ± 2.38	19–26 22.3 ± 1.71	18–28 23.4 ± 2.89 (*N* = 18)
Internasals	4 (rarely 5)	2–4 3 (*N* = 16), 4 (*N* = 20)	2–4 (mode = 4)	2–4 (mode = 4)	4 (rarely 3)
Supraoculars	3–5 (mode = 4)	5–7 (mode = 6)	4–5 (mode = 4)	4–6 (mode = 5)	5–7 (mode = 6)
Fourth finger	17–23	17–23	14–19	15–20	16–22
Subdigitals	19.7 ± 1.26	19.3 ± 1.37	17.5 ± 1.38	17.8 ± 1.34	18.9 ± 1.63 (*N* = 19)
Fourth toe	24–32	23–28	24–29	20–29	22–29
Subdigitals	27.5 ± 1.93	25.2 ± 1.55	26.5 ± 1.68	24.1 ± 1.85	25.1 ± 1.57 (*N* = 19)
Tail/total	0.66–0.71	0.63–0.70	0.64–0.67	0.64–0.70	0.63–0.70
Length	0.69 ± 0.013 *N* = 16	0.67 ± 0.015 *N* = 29	0.65 ± 0.012 (*N* = 6)	0.67 ± 0.021 (*N* = 10)	0.66 ± 0.03 (*N* = 13)
Maximum size (mm)					
Males	97	76	68	61	75
Females	82	67	61	59	71
Posthumeral pocket	Type 4 (rarely Type 3)	Type 1	Type 1 (rarely Type 2)	Type 1	Type 1
Postfemoral pocket	Type 5 (rarely Type 4)	Type 1	Type 3 (rarely Type 4)	Type 1	Types 1–3 (mode = Type 2, but high frequency of Type 3)

[1]Fritts (1974: 44, 45) reported considerable variation in some meristic counts and coloration among populations he assigned to *Stenocercus chrysopygus* (e.g., midbody scale rows, for which he reported a range of 54–82, compared to 43–67 in my sample). The sample variances for scale counts of all specimens I examined are universally higher than those for the other species in this table, thus lending credence to higher variability in *S. chrysopygus*. I have not attempted to analyze this variation and the values reported are for all specimens combined, including those questionably referred to *S. chrysopygus* (*Specimens Examined*). Fritts' (1974) discussion of this species should be used to supplement my account. However, the increased variability and interpopulational differences could also indicate that more than one species is represented by the combined populations (see text).

depth is greater than half the diameter of its opening. Type 5—a deep pocket with a narrow, slit-like opening and a depth greater than half the diameter of its opening.

Angulate temporal scales are distinctly enlarged, keeled scales posterior to, and in line with, the superciliary scales. When present, they form a distinct border between the posterior head scales and the lateral temporal scales, and they are morphologically distinguishable from these series (Cadle, 1991: 6, 7).

Coordinates for Ecuadorian localities


81°
79°
ECUADOR
PERU
4°
6°
8°
10°
Alamor
Rio Chira/
Catamayo
El Pargo
Rio Marañon
Cachil
Rio Santa
0
100
200
300
kilometers

were taken from Paynter (1993). Those for Peruvian localities were obtained from Stephens and Traylor (1983), Lamas (1976), or from departmental maps produced by the Instituto Geográfico Militar, Lima. Additional locality information was taken from Stiglich (1922). Distributions of the new species and others emphasized in this paper are given in Figure 1.

Some of the specimens referred to herein are to be returned to the Museo de la Universidad Nacional Mayor de San Marcos (MUSM; Lima, Peru). These specimens are identified with Cadle field numbers as MUSM-JEC. I used other MUSM specimens before they were cataloged into that collection, and their MUSM numbers were supplied subsequently in correspondence. To avoid possible confusion, I provide my original field numbers for these specimens (the only attached tags when I was writing the descriptions).

Other institutional abbreviations are AMNH (American Museum of Natural History, New York), ANSP (Academy of Natural Sciences of Philadelphia), BMNH (The Natural History Museum, London), LSUMNS (Louisiana State University Museum of Natural Science, Baton Rouge), MCZ (Museum of Comparative Zoology, Harvard University), MVZ (Museum of Vertebrate Zoology, University of California at Berkeley), and USNM (National Museum of Natural History, Washington, D.C.).

DESCRIPTIONS OF NEW SPECIES

Stenocercus limitaris new species

Figures 2–5; Table 1

Holotype (Figs. 2, 3). **American Museum of Natural History (AMNH) 22183. ECUADOR: Loja:** Alamor [1,325 m; 04°02′S, 80°02′W]. Adult male obtained 22–30 August 1921 by G. H. H. Tate.

Paratypes. **ECUADOR: EL ORO:** Salvias [1,050 m; 03°45′S, 79°40′W], **AMNH 18311** (11 August 1920, H. E. Anthony). **LOJA:** Alamor (topotypes), **AMNH 18319** (3 October 1920, H. E. Anthony), **AMNH 22113–19, 22131–32, 22158–62, 22165–67, 22178–82** (22–30 August 1921, G. H. H. Tate); **AMNH 22223–29** (19 September 1921, G. H. H. Tate). Piñas, 8 mi. N of Alamor[3] [3,600 ft. = 1,097 m] [04°01′S, 80°02′W], **AMNH 22215** (9 September 1921, G. H. H. Tate). Cruzpamba, 1,000 m [on the Río Celica, 04°10′S, 80°01′W], **MCZ 85083** (10 July 1965, D. Norton and P. Mattocks).

PERU: PIURA: Toronche (town at base of Cerro Aypate, approximately 16 km [airline] SE Ayabaca), 1,950–2,100 m [04°35′S, 79°32′W], **MUSM 16745–49** (JEC 10272–75, 10277, respectively), **MCZ 182245–48** (24 September 1991, J. E. Cadle). **TUMBES:** Quebrada Faical E El Caucho, 24 km SE Pampa de Hospital, 600 m [03°49′S, 80°16′W], **LSUMNS 39444** (21 June 1979, T. S. Schulenberg).

Distribution (Fig. 1). Known from southwestern Ecuador (El Oro and Loja provinces) in the upper reaches of the Río

[3] This locality is not the Piñas in El Oro province shown on most maps of Ecuador and commonly listed in gazetteers (e.g., Chapman, 1926: pl. XXX; Paynter, 1993: 157). Tate referred to the Piñas in Loja province as "Las Piñas" and reached it via trail from Alamor. A sketch map in Tate's notes shows Las Piñas approximately due north of Alamor at 3,600 ft. elevation (Tate field notes in AMNH Herpetology archives, p. 23 for 7 September 1921).

←

Figure 1. Northwestern Peru and western Ecuador showing distribution of species of *Stenocercus* emphasized in this paper. Stippled areas are above 1,000 m and hatched areas are above 3,000 m. All known localities for the new species and their type localities are indicated (see text for precise type localities): *Stenocercus limitaris* (type locality: Alamor), dots; *Stenocercus stigmosus* (type locality: El Pargo), squares; *Stenocercus latebrosus* (type locality: Cachil), triangles. Area shaded by diagonal lines between 8° and 10°S is the approximate known distribution of *Stenocercus chrysopygus* Boulenger (after Fritts, 1974), with localities for specimens examined in this study indicated by open circles. These include populations in western Ancash department questionably referred to *chrysopygus* (see text and *Specimens Examined*); note outlying eastern population in the Río Huallaga drainage (arrow at 09°46′S, 76°05′W). The approximate distribution of *Stenocercus ornatissimus* (Girard), as conceived in this paper (see text), is indicated on the inset map by solid shading (arrow).

Figure 2. Holotype of *Stenocercus limitaris* (AMNH 22183; male, SVL 91 mm).

Puyango and Río Alamor/Catamayo systems; from extreme northwestern Peru in upper reaches of the Río Quiroz system east of Ayabaca (Piura department); and from coastal drainages of Tumbes department, Peru. Ecuadorian localities are approximately 1,000–1,300 m and the Tumbes department (Peru) locality is 600 m. At Cerro Aypate near Ayabaca, Peru (Piura department), I observed *Stenocercus limitaris* between 1,930 m and approximately 2,200 m elevation.

Figure 3. The characteristic throat pattern of adult males of *Stenocercus limitaris* (holotype, AMNH 22183).

Etymology. Limitaris is Latin meaning "on the border," referring to the distribution of the species in the borderlands between Ecuador and Peru. It is used here as an adjective.

Data on the Holotype. Adult male. SVL, 91 mm. Tail length, 179 mm. Total length, 270 mm. Tail/total length, 0.66 mm. Midbody scales, 43. Gular scales between the ears, 20. Internasals, 4. Subdigital scales on fourth fingers and toes, respectively, 21-20, 27-28. The tail is cracked 81 mm from the vent. The type is dull grayish brown, and most elements of the pattern, except the light antehumeral bar and the dark patch on the throat, are obscure.

Definition. A species of *Stenocercus* characterized by the following features: (1) Dorsal head scales keeled (occasionally multicarinate), juxtaposed, and somewhat protuberant; temporals keeled, imbricate. (2) Most posterior head scales larger than anterior ones with distinct interparietal, a pair of parietals, two pairs of postparietals, and a median pair of occipitals. (3) Internasals 4 (rarely 5). (4) One row of supraoculars distinctly enlarged. (5) Two canthals on each side between the superciliaries and the postnasals or nasals. (6) A single strongly keeled angulate temporal

on each side, without projecting blade, in contact with the posterior-most postparietal. (7) Anterior gulars smooth to weakly keeled (keels more prominent in males than in females); posterior gulars strongly keeled. (8) Parietal eye distinct. (9) Neck folds absent. (10) Dorsal and ventral body scales imbricate, mucronate, and strongly keeled. (11) Vertebral row continuous, bearing a strongly projecting serrate crest in adult males, weakly projecting in females. (12) Deep posthumeral and postfemoral pockets, Types 4 and 5, respectively. (13) Scales of posterior thigh imbricate, keeled. (14) Tail strongly compressed in adult males and with a serrate dorsal crest continuous with that of the dorsum; tail weakly compressed in adult females. (15) Dorsal coloration of males brown with or without distinct chevrons, a distinct white vertical scapular stripe, and a blackish transverse bar or blotch on the throat (Fig. 3); females similar but lacking the throat blotch.

Diagnosis. In having large posterior head scales, large supraoculars, and keeled ventral scales, *Stenocercus limitaris* matches the external criteria used by Fritts (1974) to diagnose *Ophryoessoides* as distinct from *Stenocercus* (discussed by Frost [1992] and Cadle [1991]). Of species of *Stenocercus* having this combination of features, only *S. iridescens* occurs west of the Andes and, of the other species, only *S. huancabambae* occurs in adjacent parts of northern Peru (Cadle, 1991).

Stenocercus limitaris (Fig. 4) is distinguished from *S. iridescens* (characteristics in parentheses; see Cadle, 1991: fig. 10) in having smaller head plates that are keeled, wrinkled, or multicarinate (head plates large, smooth); generally 5 or 6 scales across the top of the head in a transverse row between the canthals, all more or less equal in size (2–4 scales, including two greatly enlarged median scales); and generally a continuous ring of small scales separating the enlarged supraocular rows from the median head scales (ring often incomplete but always reduced to tiny scales).

Stenocercus limitaris is distinguished from *S. huancabambae* (contrasting characters in parentheses; see Cadle [1991: fig. 8]) in having 2 median posterior occipital scales (usually 3), 2 canthals (1), lacking a row of small scales medial to the angulate temporal scale (present; see Cadle [1991: 31, 32] for discussion), having a black transverse bar or large blotch on the throat in males (black longitudinal streak), and having a short antehumeral light bar that ends on the base of the forelimb (antehumeral bar longer, extending onto upper forelimb).

Other species of *Stenocercus* with enlarged posterior head scales and keeled ventrals [*aculeatus* (O'Shaughnessy), *caducus* (Cope), *dumerilii* (Steindachner), *erythrogaster* (Hallowell), *fimbriatus* Avila-Pires, *scapularis* (Boulenger), *tricristatus* Duméril] occur on the Amazonian slopes or lowlands and differ from *S. limitaris* in coloration and in having dorsolateral (as well as vertebral) crests on the body (see Avila-Pires, 1995; Cadle, 1991: 36, 37).

Stenocercus limitaris differs from other species of *Stenocercus* occurring in Peru and Ecuador in having the combination of deep posthumeral (Type 4) and postfemoral (Type 5) pockets, enlarged posterior head scales, a projecting vertebral crest (especially in adult males), and keeled ventrals. Three species of southern Ecuador and northern Peru, *S. rhodomelas, S. ornatus,* and *S. percultus,* have deep posthumeral pockets and projecting vertebral crests; these species are distinguished from *S. limitaris* by aspects of coloration and in having smooth ventrals (see Fritts, 1974; Cadle, 1991: 27).

Description. Head. Dorsal head scales juxtaposed, and keeled, wrinkled, or multicarinate (Fig. 4). Supraoculars, in particular, tend to be multicarinate. Keels or wrinkles much more prominent in juveniles than adults. Rostral in contact with first supralabial, first lorilabials, postros-

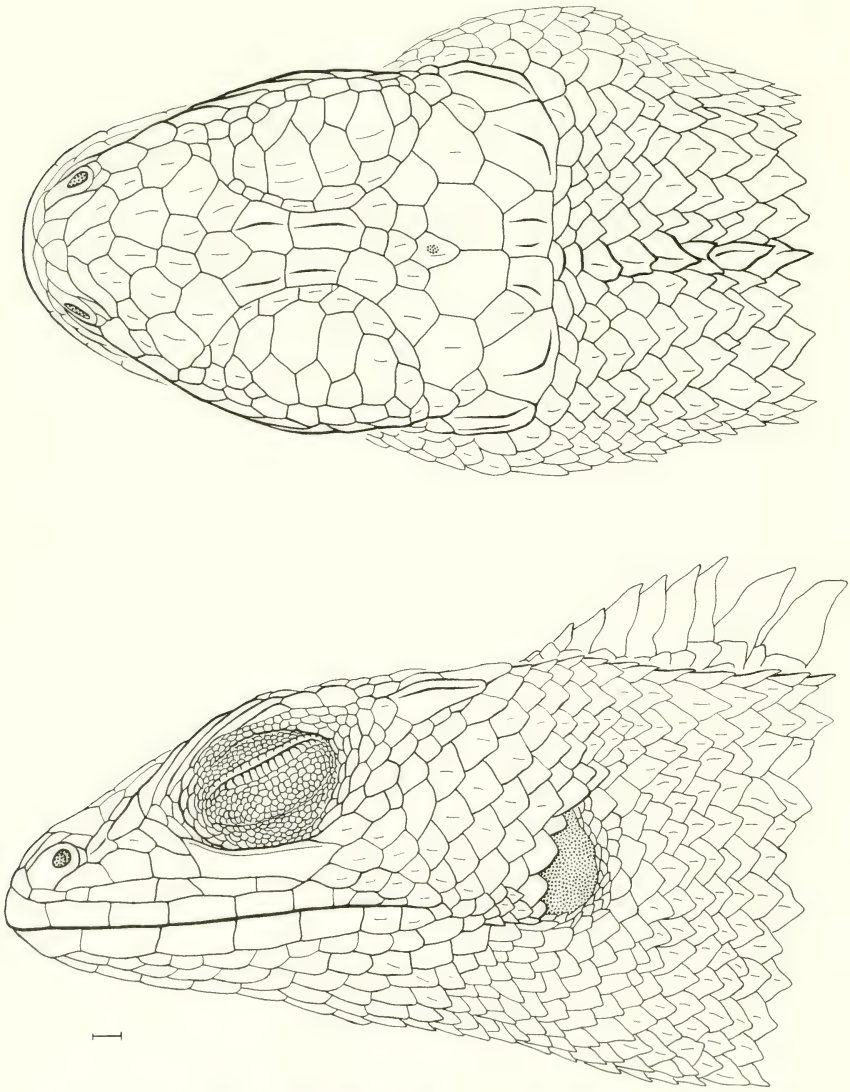


Figure 4. *Stenocercus limitaris* (holotype, AMNH 22183). Dorsal and lateral views of head scales. Bar = 1 mm.

trals, and occasionally the internasals. Medial postrostrals short, irregularly trapezoidal, occasionally failing to meet on the midline. Two canthals anterior to the superciliary series, the anterior ones in contact with the nasals or separated from them by tiny scales. Four elongate superciliaries overlapping posteriorly, followed by 2 or 3 shorter posterior superciliaries overlapping in the reverse direction. Internasals 4 (rarely 5). One row of enlarged supraoculars. Parietal region with distinct interparietal, a pair of parietals, two pairs of postparietals, and a pair of occipitals. Parietals are in contact on the midline, but both pairs of postparietals are separated by the occipitals; anteromedial postparietals less than half the size of the posterolateral postparietals. Parietal eye visible.

Temporal scales keeled, imbricate. Lateral temporal scales separated from posterior dorsal head scales on each side by a single, elongate, strongly keeled angulate temporal scale. The angulate temporal is in contact with the second postparietal and one or two other posterior head scales (not separated from enlarged posterior head scales by a row of small scales, as in some other species of *Stenocercus*). Although the angulate temporal is strongly keeled, it does not bear a projecting vane as in *S. iridescens* and *S. huancabambae* (Cadle, 1991).

Anterior gulars weakly keeled or smooth, those posterior to the level of the anterior edge of the ear strongly keeled. Mental in contact with first pair of postmentals and first pair of infralabials. Enlarged postmentals 4 or 5 on each side, the first pair in contact medially.

Neck and Body. Dorsal and lateral scales of neck and body imbricate, mucronate, strongly keeled. Vertebral row produced into a prominent projecting serrate dorsal crest in adult males that is continuous from the nuchal region to approximately the basal one-third of the tail; crest projecting, but less so, in females. No dorsolateral crest. Pre-auricular fringe well developed; posterior border of ear smooth. Ventral body scales mucronate, strongly keeled, approximately the same size as the dorsals.

Neck Folds. Distinct neck folds absent. At most, very slight indications of antehumeral and dorsolateral folds.

Tail. Tail strongly compressed in adult males, less so in females; bearing projecting crest continuous with that of the body. Dorsal and ventral scales similar to those of the body.

Limbs. Dorsal and ventral scales of fore- and hindlimbs, and posterior thigh strongly keeled, mucronate. Supradigitals and subdigitals of both limbs keeled. Plantar and palmar scales strongly keeled.

Posthumeral and Postfemoral Mite Pockets. Posthumeral and postfemoral mite pockets deep (Types 4 and 5, respectively).

Size and Proportions. Largest male (AMNH 22183) SVL 91 mm. Largest female (MCZ 182246) SVL 82 mm. Tail 66–70% of total length.

Coloration and Pattern in Life. Adult Males. I have not collected adult males of *Stenocercus limitaris* but at Toronche (Piura department, Peru) I observed an adult male and one apparently subadult male. The adult male had a projecting vertebral crest and a black bar below the eye. There appeared to be two wide black vertical bars in the shoulder region highlighting the light scapular stripe. The subadult had a black suborbital bar and a black scapular spot bordering the posterior edge of the scapular stripe. The black spot did not have a distinct posterior border, but faded into the brown flank color. A series of dark middorsal chevrons on the brown ground color was evident in the subadult.

Adult female (Fig. 5, based on MCZ 182246 from Toronche, Piura department, Peru) SVL 82 mm. Top of head and dorsum medium brown. Dorsum with brown chevrons, very indistinct anteriorly, becoming discrete on posterior dorsum, pelvis, and tail. Side of neck and flanks rich yellowish brown. Loreal region and upper labials dull yellowish white. Small scales

Figure 5. Adult female of *Stenocercus limitaris* in life (MCZ 182246 from Toronche, Piura department, Peru). Note the lack of neck folds, the light antehumeral bar ending at the base of the forelimb, and the dark subocular bar characteristic of this species.

dorsal and posterior to angle of mouth orangish. Black vertical bar across eyelids continuing to upper labials. Light yellowish vertical stripe in scapular region. Dorsal surfaces of limbs brown; thighs indistinctly barred with darker brown. Throat and pectoral region grayish white washed with yellowish. Belly, ventral limbs, and ventral tail grayish tan, unmarked. A vague light (yellowish brown) stripe at upper edge of posterior surface of the thigh, slightly outlined with darker pigment (which is the only reason it is at all discrete).

Another female (MUSM 16749, SVL 67 mm) and two subadults (MCZ 182247–48, SVLs 45–50 mm) from the same locality as MCZ 182246 are similar to the latter except the colors are duller. The dorsal chevrons in the two subadults are much more distinct than in the two larger females and the flanks of the subadults are darker. Another female (MCZ 182245, SVL 72 mm) has much dark gray pigment on the ventral surface of the head and neck; the pigment is denser on the neck, forming an indistinct dark collar on the throat. The stripe on the posterior surface of the thigh is obvious on all individuals but more evident in the subadults.

Coloration in Preservative. Dull grayish brown or brown with darker brown markings. The suborbital dark bar, light antehumeral bar, and dark blotch on the throat of males usually are evident but other pattern elements are obscure. Some females retain dark mottling on the gular and ventral neck regions. Some preserved males (e.g., MCZ 85083, LSUMNS 39444) and females (e.g., AMNH 22160) have light spots on a generally darkened pectoral region. The light postfemoral stripe is retained in well-preserved recent specimens of both sexes (all paratypes from Peru and from Cruzpamba, Ecuador) and in many older specimens. It is evident as an indistinct light stripe or series of spots bordered by slightly darker scales.

Scale Counts and Qualitative Features (Table 1). Stenocercus limitaris has low numbers of body scales compared to many species of *Stenocercus,* indicating that the scales are large for a lizard of this size. The scale counts, size, and the posthumeral and postfemoral mite pockets are very similar to those of *S. huancabambae* (Cadle, 1991: table 1).

Sexual Dimorphism and Geographic Variation. Stenocercus limitaris exhibits strong sexual dimorphism. Males have a strongly projecting serrate vertebral crest from the nape well onto the tail. In females the crest is present but very reduced. The sexes also differ in coloration, although the lack of detailed observations on male colors in life make this difficult to assess. Females lack the dark blotch on the throat characteristic of males, and the light scapular stripe is more prominent in males because of its contrasting border of dark pigment. Males attain a slightly larger size than females (Table 1) and are somewhat more robust. Males and females do not differ significantly in meristic counts.

Only two populations (Alamor, Ecuador, and Toronche, Peru) are represented by enough specimens to assess interpopulational differences statistically. Although separated by only a distance of approximately 80 km (airline), the terrain in this area is heavily dissected by rivers flowing

from the Andes. The great Río Chira/Catamayo system and its tributaries separate Alamor and Toronche (Fig. 1). The only significant meristic difference between these two populations is the mean number of midbody scale rows ($\bar{x}$ = 46.3 ± 2.83 vs. 50.1 ± 2.42 for Alamor and Toronche, respectively; $t = 3.63$, $P < 0.001$). Despite statistical significance, the ranges of midbody scales for these populations (39–53 vs. 47–54, respectively) entirely overlap.

Natural History. Most of the type series of *Stenocercus limitaris* was obtained by G. H. H. Tate while collecting birds and mammals for the American Museum of Natural History in western Ecuador (Chapman, 1926). Tate worked at the type locality and nearby sites from 14–31 August and 4–20 September 1921 (Chapman, 1926: 16). Chapman (1926: 703) described Alamor thus: "altitude 4550 ft. [1387 m], a small town lying along a ridge between the Ríos Tumbez and Alamor. Heavy subtropical forest lies west and north of Alamor and humid tropics may be quickly reached in the valleys below." H. E. Anthony, who worked at Alamor 30 September–5 October 1920, described the area as follows (H. E. Anthony, unpublished summary of field work in Ecuador, Mammalogy Department, AMNH):

> Alamor . . . is on the border line between the arid tropical and the humid tropical. The great forests which clothe the western Andes have their eastern limit at this point, and with their southern limit as well not much to the south of Alamor. West of this little hill it is possible to enter splended tropical forest . . . . To the north the forest reaches greater elevations and much of it is subtropical to temperate.

Since the 1920s, the great tropical and temperate forests of western Ecuador described by Chapman and Anthony have been destroyed (Dodson and Gentry, 1991).

I have few natural history observations on *Stenocercus limitaris*. The tag of LSUMNS 39444 states that it was collected in humid deciduous forest. At Toronche (Piura department, Peru) all *S. limitaris* I observed were in a heavily disturbed area of second growth, pastures, and agricultural land. However, the native habitat may have been a more humid forest, as the summit of nearby Cerro Aypate was covered with a wet montane forest as late as 1991 (Gentry, 1995; personal observations). Most of the lizards were among thickets and fencerows along trails or roads and took refuge in debris piles or under objects on the ground. One individual took refuge in a crevice in a vertical roadcut, but in general these animals do not seem to be climbers. They are wary lizards and are difficult to approach when they are active.

Around the base of Cerro Aypate I observed many individuals of *Stenocercus limitaris*, including adults of both sexes, on a hot afternoon with bright sun. However, the following day was overcast and somewhat cool, and few lizards (all females and subadults) were seen. Local informants stated that they are out in abundance only on very hot days.

Stenocercus limitaris is known to be sympatric with other species of *Stenocercus* at Quebrada Faical (Tumbes department, Peru), where *Stenocercus iridescens* also occurs,[4] and at Alamor (type locality),

[4] Specimens of *Stenocercus iridescens* from Quebrada El Faical (LSUMNS 39443, 39445–47, 39451) and another from a nearby locality (LSUMNS 26989) differ from typical *S. iridescens* in lacking distinct black markings on the throat. The El Faical specimens show a general darkening of the throat and pectoral region, with large unpigmented spots across the pectoral region. This is unusual for *S. iridescens* and these specimens were thought by E. E. Williams (personal communication) to represent a distinct species. However, my survey of *S. "iridescens"* in the MCZ suggests much variation in throat pattern and also the degree of keeling on the ventral scales, perhaps attributable to a combination of preservation artifact and geographic or other significant variation. Specimens from the Río Cazanga valley (Loja province, Ecuador; MCZ 85089–90, 131822) are similar to the El Faical specimens in having smooth ventrals, but MCZ 85089–90 (adult males) have a dark median spot on the throat, unlike the transverse band or paired blotches characteristic of typical *iridescens*. Other specimens (e.g., MCZ 145370; Pichincha prov-

where *S. carrioni* also occurs (MCZ 34866, 133220; exchanged to MCZ from Tate's AMNH collections, where a large series of *carrioni* resides [Fritts, 1974]).

Remarks. Stenocercus limitaris was recognized as new by P. E. Vanzolini and E. E. Williams many years ago on the basis of Tate's collections and others from Ecuador. They had labeled specimens from some collections, perhaps including some not studied herein, as "*Stenocercus orcesi*," which they had intended to name this species.

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ince, Ecuador) have strongly keeled ventrals and a generally dark venter. Until variation in *iridescens* is more thoroughly studied, I hesitate to attribute significance to these differences.

Stenocercus latebrosus
new species
Figures 6–12; Tables 1–3

Holotype (Fig. 6). **Museo de Historia Natural de San Marcos (MUSM) 16744** (field number JEC 13026). **PERU: CAJAMARCA:** Bosque de Cachil, approximately 3 km (airline) SE Contumazá, 2,500 m [07°23'S, 78°47'W]. Adult male collected 17, 18 August 1994 by John E. Cadle, Pablo Chuna, and Segundo Leiva.

Paratypes. **PERU: CAJAMARCA:** Same data as the holotype, **MUSM-JEC 13014, 13021–22, 13024, 13027, 13029**; **MCZ 182236–41**. Same locality as the holotype but 2,400–2,420 m, **MCZ 178040–43** (27 July 1993, P. Chuna, P. Lezama, S. Leiva); **MCZ 178044** (17 May

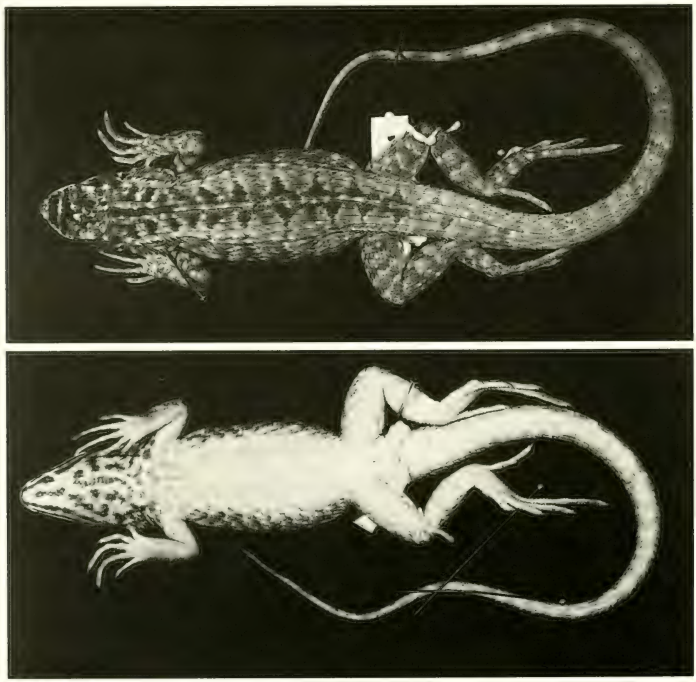

Figure 6. Holotype of *Stenocercus latebrosus* (MUSM 16744; adult male, SVL 68 mm). Dorsal and ventral views.

1993, P. Chuna, P. Lezama); **MCZ 178048–49**, **MUSM-JEC 10323** (28 September 1991, J. E. Cadle and P. Chuna); **MCZ 178268–70** (13 December 1993, P. Chuna). Carabamba, Provincia Cajabamba [approximately 07°33′S, 78°15′W],[5] **MCZ 154240** (2 November 1967, P. M. Lujan). San Pablo [2,400 m;[6] 07°07′S, 78°50′W], **BMNH 1900.3.30.14** (5 November 1899, P[erry] O. Simons). **LA LIBERTAD:** 5 mi. SW Otuzco, 8,000 ft. [2,440 m; approximately 07°55′S, 78°33′W], **MVZ 119233–36** (31 August–3 September 1969, R. Hilborn, C. B. Koford, and M. Leong). Mountain ridge above Sinsicap, 2,400–2,600 m [07°50′S, 78°45′W], **MUSM-JEC 13836, 13838–40**, **MCZ 182242–44** (9 July 1995, J. E. Cadle, P. Chuna, S. Leiva, and P. Lezama).

Referred Specimens. Specimens from the vicinity of Otuzco (La Libertad department, Peru) appear to be relatively common in various collections, but I have not made a comprehensive survey of all specimens and have specifically examined only those listed as types. Fritts (1974) based his discussion of *Stenocercus ornatissimus* primarily on specimens (apparently) of *S. latebrosus* from near Otuzco (KU 134351–78, not examined in this study). His photograph of "*ornatissimus*" from Otuzco (Fritts, 1974: 78, fig. 25) in actuality appears to be *latebrosus,* as indicated by the distinctively patterned head and dorsum. *Stenocercus ornatissimus* and *S. latebrosus* are very similar (see below), but differ in several qualitative characters. *Stenocercus ornatissimus,* in my conception, is presently known only from Lima department, far south of the only known localities of *latebrosus* in Cajamarca and La Libertad departments (Fig. 1).

Distribution (Fig. 1). *Stenocercus latebrosus* is known from the Cordillera Occidental of the Andes in southern Cajamarca and western La Libertad departments, Peru (Pacific slopes drained by the Río Chicama and Río Chilete); and from the main portion of the Cordillera Occidental in extreme southeastern Cajamarca department (Amazonian slope). The known elevational range is approximately 2,400–2,600 m.

Etymology. The species epithet *latebrosus* is a Latin adjective meaning "full of hiding places," an allusion to the deep mite pockets concealed among the neck folds of this species.

Data on the Holotype. Adult male with everted hemipenes. SVL, 68 mm. Tail length, 147 mm. Total length, 217 mm. Tail as a percentage of total length, 68%. Midbody scales, 41. Gular scales between the ears, 20. Internasals, 4. Subdigital scales on fourth fingers and toes, respectively, 19-20, 28-29.

Definition. A species of *Stenocercus* characterized by the following features: (1) at least posterior scales on top of head keeled, juxtaposed; temporals keeled, slightly imbricate (Fig. 7). (2) No distinct parietals, postparietals, or occipitals; posterior head scales small; interparietal small, irregular, indicated by visible parietal eye. (3) Internasals usually 3 or 4. (4) No supraocular row distinctly enlarged, although supraoculars vary in size. (5) Two canthals on either side between the superciliaries and the postnasals. (6) No distinct angulate temporals; temporal and posterior head scales strongly keeled. (7) Gulars and postmental series smooth. (8) Parietal

[5] MCZ catalogs record La Libertad department for this locality but Provincia Cajabamba is in extreme southeastern Cajamarca department adjacent to La Libertad.

[6] Simons' field tag attached to the specimen and the BMNH catalog give 3,000 m as the elevation of San Pablo. However, Stephens and Traylor (1983) give 2,365 m and I recorded 2,400 m when I visited San Pablo in 1994. Perry O. Simons collected specimens (primarily mammals) from the Andes of Ecuador, Peru, Bolivia, and Argentina for the British Museum (Natural History) from November 1899 to November 1901. The herpetological collections were described by Boulenger (1899, 1900, 1901), the mammal collections by Thomas (1901, 1902a, b), and the bird collections by Chubb (1919). Chubb (1919) gives an itinerary and list of Simons' localities based on his diaries. The date of collection for BMNH 1900.3.30.14 is that given in Chubb's itinerary for the date when Simons was in San Pablo.

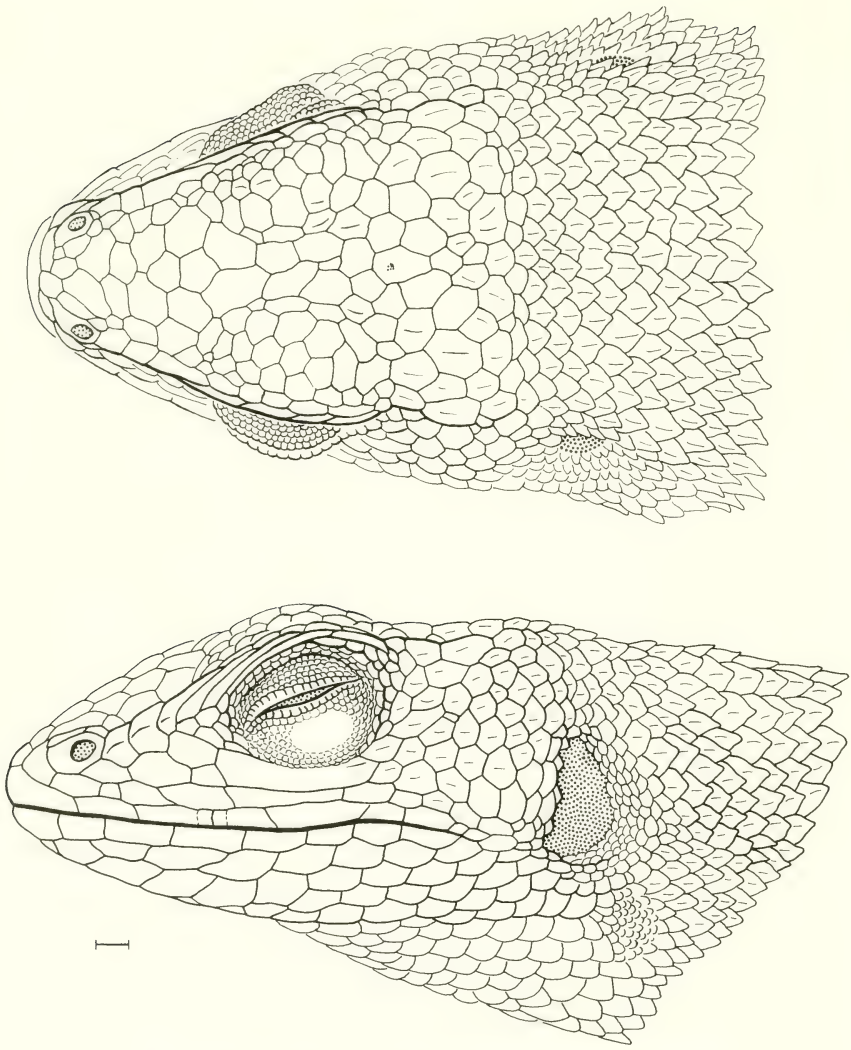

Figure 7. *Stenocercus latebrosus* (paratype, MCZ 154240). Dorsal and lateral views of head scales. Bar = 1 mm.

eye distinct. (9) Antehumeral and oblique neck folds very strongly developed, although this may not be superficially evident because of the heavy covering of large, strongly keeled, mucronate scales on the side of the neck. Other neck folds not distinct. Deep mite pockets present under the antehumeral and oblique neck folds, the oblique neck pocket much larger than the antehumeral pocket. (10) Dorsal scales imbricate, mucronate, and strongly keeled. (11) Vertebral row continuous, not differentiated from paradorsal rows and not bearing a projecting crest. (12) No posthumeral or postfemoral pockets (Type 1). (13) Scales of posterior thigh granular. (14) Tail slightly compressed. (15) Dorsal coloration similar in males and females: brown with paired middorsal series of dark brown triangles or diamonds; dorsolateral light brown stripes distinct in females, less so in males. Gular region of males whitish with black reticulations, which may be so extensive as to make the throat appear black with large whitish spots. Gular region of females white with scattered black spots.

Diagnosis. The presence of deep mite pockets underneath the antehumeral neck folds and the oblique neck folds (Fig. 12) distinguishes *Stenocercus latebrosus* from all other species of *Stenocercus* except *S. ornatissimus.* Although mite pockets underneath neck folds are present in many species of *Tropidurus* (Rodrigues, 1987; Frost, 1992), they are otherwise rare among iguanians. Cadle (1991) found shallow mite pockets under the antehumeral folds in some individuals of *Stenocercus eunetopsis, S. simonsii, S. carrioni, S. cupreus,* and *S. chrysopygus.* The mite pockets in these species are present only in some adults and are little more than bare skin with a slight overhang of the antehumeral folds (with the exception of some populations of *S. chrysopygus,* in which they are more extensive; see footnote 7). The deep mite pockets underneath the antehumeral and oblique neck folds in *Stenocercus latebrosus* are consistently present in all individuals, even hatchlings and small juveniles. The neck mite pockets of *S. latebrosus* are so distinct that the first specimens I collected, all small juveniles, were immediately tentatively recognized as a new species based solely on the presence of these pockets, which were densely packed with bright red mites. In degree of development and consistency of presence, the neck mite pockets of *S. latebrosus* are approached only in *S. ornatissimus* (see following detailed comparison of these two species).

Aside from *Stenocercus ornatissimus, S. latebrosus* is most easily confused with *S. chrysopygus. Stenocercus latebrosus* averages fewer scales around midbody than *S. chrysopygus* (44 vs. 52, respectively; Table 1), and *latebrosus* lacks a postfemoral mite pocket (Type 1), whereas at least topotypic *chrysopygus* have a postfemoral pocket of Type 2 or 3. Some *chrysopygus* have weakly to strongly developed pockets under the antehumeral folds, but not under other neck folds, in particular the oblique fold, which in *laterbrosus* conceals a very deep mite pocket.[7] Adult males of *chrysopygus*

[7] The variation in both qualitative (posthumeral and postfemoral pockets, neck pockets) and quantitative (scale counts; Table 1) characters in *chrysopygus* makes precise diagnosis difficult. Specimens from some populations that I tentatively refer to *chrysopygus* lack postfemoral pockets entirely, whereas in others, the pocket consists of a bare skin patch occasionally with a slight overhanging fold. These pockets are always poorly developed in topotypic *chrysopygus.* Similarly, the extent of development of the neck mite pockets varies considerably. For example, topotypic *chrysopygus* generally have a weakly developed pocket under the antehumeral fold, whereas specimens from near Pariacoto and Marca (Ancash department; BMNH, MVZ, and LSUMNS specimens) have very deep pockets under the antehumeral fold equal to, or greater than, its development in *ornatissimus* or *latebrosus.* Color patterns and meristic differences also vary greatly among populations referred to *chrysopygus,* as also noted by Fritts (1974). In general, the extensive variation among populations assigned to *chrysopygus* suggests to me that more than one species may be represented (Table 1), but the variation has not yet been studied systematically. Some of these "*chrysopygus*" populations may not be diagnosable from *ornatissimus.* These problematic

lack the bold black reticulations or large white spots on a black ground color characteristic of *latebrosus* (see *Coloration and Pattern in Life*).

Description. Head. Dorsal head scales small, juxtaposed, and usually strongly keeled, except for some supraoculars and scales on top of the snout (Fig. 7). Extent of keeling varies, but not consistently according to sex or size (see *Sexual Dimorphism and Geographic Variation*). At least the posterior head scales and some supraoculars are keeled in all specimens; supraoculars multicarinated in some specimens; keeling sometimes more extensive in juveniles. Parietal region with many small, irregular scales. Rostral in contact with first supralabial, first lorilabials, postrostrals, and occasionally the nasals. Medial postrostrals much longer than wide, in contact with rostral, internasals, and first lorilabials. Two canthals anterior to the superciliary series, the anterior ones in contact with the nasals or separated from them by tiny scales. Four or 5 elongate superciliaries overlapping posteriorly, followed by 2 shorter posterior superciliaries overlapping in the reverse direction. Internasals 3 or 4 (rarely 2). No distinctly enlarged supraoculars. Parietal, postparietals, and occipitals indistinct; posterior head scales small, fragmented. Interparietal distinguished by a distinct parietal eye visible in all specimens. Temporal scales strongly keeled, imbricate. Gulars smooth. Mental in contact with first pair of postmentals and first pair of infralabials. Enlarged postmentals 3 or 4 on each side.

Neck and Body. Dorsal scales of neck, body, and tail imbricate, mucronate, and strongly keeled down to ventrolateral junction with ventral scales. Vertebral row not, or only slightly, differentiated from adjacent rows; perhaps slightly more prominent from populations south of the Río Chicama. No projecting vertebral or dorsolateral crests. Preauricular fringe moderately developed, consisting of 3–5 scales; posterior border of ear smooth. Ventral scales of gular region and body smooth, smaller and less mucronate than dorsals.

Neck Folds. Lateral scales of neck large, mucronate, strongly keeled, concealing deep mite pockets underneath the antehumeral and oblique neck folds (Fig. 12); deep portions of mite pockets without scales, with fine granular scales peripherally. Antehumeral and oblique neck folds strongly developed, but may be concealed by the large mucronate scales of the neck. Other neck folds not evident. The scales covering the exterior of the oblique pocket posteriorly overlap those covering the antehumeral pocket (Fig. 12), thus obscuring the opening to the oblique pocket. The mite pockets underneath the neck folds are described in detail later (see *Discussion: Comparison of* Stenocercus latebrosus *and* Stenocercus ornatissimus).

Tail. Dorsal and ventral scales of tail strongly keeled and mucronate, except for a few postanal scales. Tail slightly compressed.

Limbs. Dorsal and ventral scales of forelimbs strongly keeled, mucronate. Dorsal scales of hindlimbs strongly keeled, mucronate; ventral scales smooth. Scales on posterior surfaces of thighs finely granular. Supradigitals of forelimbs smooth, of hindlimbs mostly keeled. Subdigitals multicarinate. Plantar and palmar scales strongly keeled.

Posthumeral and Postfemoral Mite Pockets. Posthumeral and postfemoral mite pockets absent (Type 1). Scales in axillary and postfemoral regions finely granular.

Size and Proportions. Largest male (MUSM-JEC 13836) SVL 76 mm. Largest female (MCZ 178040) SVL 67 mm. Tail 63–70% of total length.

Coloration and Pattern in Life. Adult Males. (Figs. 6, 8, 9), based on specimens from the type locality) dorsal ground color rich brown (somewhat chestnut) with a series of dark brown blotches middorsally. These blotches sometimes take the form

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populations are in western Ancash and eastern Huánuco departments, as discussed later.

Figure 8. Adult male of *Stenocercus latebrosus* in life (MUSM-JEC 13026 from the type locality). Note the characteristic labial markings, and that the oblique neck fold and mite pocket are obscured by large, overlying imbricate scales.

of a paired series of dark brown triangles on either side of middorsal line, separated by a fine yellowish brown line. Sometimes they are irregular markings or alternate from side to side. Each blotch has a light brown border about ½ scale wide. The size and number of the dorsal blotches vary, but the usual number between the limbs is 4 to 6. Top of head blackish brown with irregular lighter brown markings. Dorsal pattern continues onto tail, giving it an appearance of being somewhat banded or having dorsal triangular blotches. Top of limbs brown, indistinctly barred. Superciliaries tannish. Whitish bar between eye and supralabials. Supra- and infralabials blackish brown, which is emphasized by adjacent white bars (Fig. 8). Throat and ventral neck white with blackish brown longitudinal and diagonal streaking. Flanks dirty whitish, lighter than dorsum. Pectoral region, venter, ventral surfaces of hind limbs (especially thighs), and base of tail washed with brilliant yellow and occasional bluish streaks. Remainder of ventral surface of tail indistinctly barred with dirty white bands (1 scale wide) alternating with gray bands (about 2 scales wide). In some males, the brilliant yellow wash covers much of the head, especially the loreal/subocular bar, superciliaries, mental region, and auricular region (sometimes also the top of head).

Males from near Sinsicap (La Libertad department) are similar to those from the type locality, except the black throat markings are so extensive that they anastomose to give the appearance of a black throat with large white spots (Fig. 9). Males from this population, and occasional male topotypes, had bright sky-blue flecks dorsally on the neck and anterior body. These flecks were occasionally arrayed in paired dorsolateral series (e.g., MUSM-JEC 13836, MCZ 182240).

The single male from San Pablo is similar to the Cachil specimens in throat pattern, so it appears that populations on the Pacific versant north of the Río Chicama have bold, nonanastomosing reticulations on the throat, whereas those from south of the Río Chicama have anastomosing reticulations enclosing white spots. The single available specimen from the Amazonian versant (MCZ 154240) is similar to the southern populations in throat pattern.

Adult Females in Life (based on specimens from the type locality). Pattern similar to males with some exceptions: (1) Females lack the yellow wash on the venter and head; (2) Females tend to have, in addition to the dorsal dark blotches, dorso-

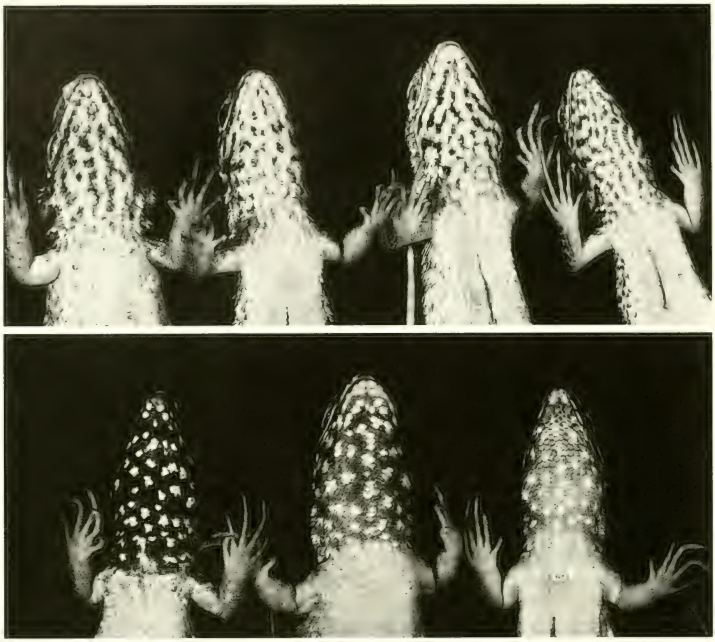

Figure 9. Variation in throat patterns of adult males of *Stenocercus latebrosus* from two localities. Top panel, four specimens from the type locality, Bosque de Cachil (left to right, MCZ 182240, 182238, MUSM-JEC 13014, MCZ 182241). Bottom panel, three specimens from the vicinity of Sinsicap (left to right, MCZ 182242, MUSM-JEC 13836, MCZ 182243).

lateral light stripes that begin above the ear (or slightly anterior), and fade on the base of the tail; these stripes are grayish white to yellowish brown and are widest at midbody; (3) Some females have a slightly orangish wash at the lower edge of the flanks/extreme lateral edge of the belly (in MCZ 182239, most of belly and ventral side of tail had this wash); (4) Dark markings on throat are less bold in females than in males (Fig. 10). Females with the orange wash on the flanks and belly were gravid and the coloration may be correlated with this condition.

Figure 10. Variation in throat patterns of adult females of *Stenocercus latebrosus* (left to right, MCZ 182236–237, 182244).

Subadults in Life (based on MCZ 178048–49, MUSM-JEC 10323; SVLs 36–43 mm). Dorsal ground color brown with series of dark brown chevrons that are incomplete middorsally (appearing as a paired series of irregular dorsolateral spots). Light dorsolateral stripe grayish tan. Dorsal surfaces of head and limbs brown with few dark flecks. Flanks brown, heavily speckled with darker brown and lighter (grayish) flecks. Gular, throat, and

Figure 11. Hemipenis of *Stenocercus latebrosus* (MCZ 182242) in "lateral" (*left*) and sulcate (*right*) views. Proximal end is toward the bottom, distal toward the top. In the lateral view the sulcate surface is to the left, asulcate to the right. Details of structure visible include the "girdle" on the asulcate surface, the fine flounces at the base of the lobes on the sulcate surface, and the sulcus spermaticus.

pectoral regions whitish with irregular dark gray lines and spots; these are most distinct in the smallest individual, less so in the medium sized specimen, and least so in the largest. Ventral belly, tail, and limbs dull whitish with indistinct darker flecks in MUSM-JEC 10323, unmarked in the others.

Hatchlings in Life (from the type locality; SVLs 28–33 mm). Pattern similar to females, but hatchlings tend to be grayish brown dorsally, rather than brown (top of head and neck medium brown, unmarked). Dorsolateral stripes whitish. Throat markings indistinct.

Coloration in Preservative. Grayish brown to brown with dark brown or black markings. Bright colors (yellow and orange) are lost, but the bluish flecks on dorsal neck scales of some males are manifested by light bluish-gray scales.

Scale Counts and Qualitative Characters (Table 1). Stenocercus latebrosus has relatively low scale counts and a relatively long tail and lacks any trace of posthumeral or postfemoral mite pockets.

Hemipenis (Fig. 11). Two everted hemipenes of *Stenocercus latebrosus* were examined, one from a topotype (Cachil) and the other from a paratype from above Sinsicap (MUSM-JEC 13014 and MCZ 182242, respectively). Both everted organs were identical in essential details. The hemipenes of MCZ 154240, the only specimen from the Amazonian versant, are partially everted to the base of the lobes. All observable characters for this specimen are identical to those of the everted organs.

The hemipenis is approximately one-third bilobed and the sulcus spermaticus divides at the separation of the lobes. The basal undivided portion of the organ bears a thickened, rugose band of tissue (girdle) across the proximal portion of the asulcate surface (Fig. 11). Under high magnification this girdle seems to have thick papillae and ridges. Otherwise the undivided portion of the hemipenis is essentially nude, but there are a few fine folds of tissue adjacent to the sulcus spermaticus.

Each lobe is bulbous at its base, tapering to a pointed tip that is deflected back toward the sulcate side (Fig. 11). On either side of the sulcus spermaticus at its point of division (i.e., at the base of each lobe adjacent to the sulcus) is a series of flounces (horizontal, partially overlapping ridges); occasional connecting ridges between the flounces give the appearance of incipient calyces. Toward the asulcate side, the flounces dissipate abruptly, but a series of about three rows remains immediately below the crotch on the asulcate side. The flounces are much more prominent and regular in the Sinsicap specimen than in the Cachil specimen. Passing distally on the sulcate side, the flounces continue adjacent to the sulcus spermaticus for a distance of one-third (Cachil specimen) or one-half (Sinsicap specimen) the length of each lobe. They eventually merge imperceptibly into the calyces.

Aside from the thick branches of the sulcus spermaticus and the flounced areas on the sulcate side, the lobes are entirely calyculate and the calyces bear a dense covering of fine, pointed spinules. The spi-

TABLE 2. GEOGRAPHIC VARIATION IN MERISTIC CHARACTERS AMONG POPULATIONS OF *STENOCERCUS LATEBROSUS* NORTH AND SOUTH OF THE RIO CHICAMA (SEE TEXT FOR SAMPLES INCLUDED IN EACH POPULATION). FOR EACH CHARACTER THE MEAN ($\bar{X}$), SAMPLE VARIANCE (s^2), SAMPLE SIZE (N), AND RANGE ARE GIVEN, AND THE RESULTS OF A T TEST COMPARING THE POPULATION MEANS (DF, DEGREES OF FREEDOM).

Character	North	South	t	df	
Midbody scales	$\bar{X} = 40.6$	$\bar{X} = 48.6$			
	$s^2 = 8.07$	$s^2 = 13.86$	7.07	34	$P < 0.001$
	$N = 25$	$N = 11$			
	38–46	43–57			
Dorsal scales	$\bar{X} = 46.9$	$\bar{X} = 50.5$			
	$s^2 = 6.86$	$s^2 = 5.48$	3.84	33	$P < 0.001$
	$N = 24$	$N = 11$			
	43–52	46–53			
Gular scales	$\bar{X} = 20.1$	$\bar{X} = 22.8$			
	$s^2 = 1.33$	$s^2 = 2.56$	5.73	34	$P < 0.001$
	$N = 25$	$N = 11$			
	18–22	21–26			

nules do not seem to be calcified, as they did not stain with alizarin red. The calyculate areas of the lobes are not confluent since the crotch of the organ is nude and the calyces do not extend below the lobes.

Sexual Dimorphism and Geographic Variation. Males and females of *Stenocercus latebrosus* are similar in coloration, but the markings of males tend to be more distinct, especially those on the throat (Figs. 9, 10; See *Coloration and Pattern in Life*). Males attain larger sizes than females (Table 1) and are somewhat more robust.

The known localities for *Stenocercus latebrosus* in La Libertad department are separated from the type locality by the broad, dry valley of the Río Chicama. The samples north of the Rio Chicama (Bosque de Cachil and San Pablo) differ significantly from those south of the Río Chicama (vicinity of Sinsicap and Otuzco) in the gular pattern of adult males (See *Coloration and Pattern in Life*; Fig. 9) and in the mean number of midbody, dorsal, and gular scales (Table 2) (the single specimen, MCZ 154240, from east of the continental divide, was ignored in these comparisons). Other tabulated meristic counts (finger and toe subdigitals, supraoculars, internasals, and canthals) do not differ significantly between the populations.

The extent of keeling of scales on top of the head varies among populations. In specimens from the type locality, keels are often present on all dorsal head scales, whereas in specimens from the vicinity of Otuzco and Sinsicap (i.e., south of the Río Chicama) keels are usually restricted to posterior head scales and the supraoculars. The keels in some specimens from the last populations also seem less prominent than those in topotypes, in some instances being low, rounded, and perhaps more accurately described as wrinkles. Subadults and females from south of the Río Chicama often have a dark gray or blackish wash on the side of the head and neck between the eye and forelimb, which is bordered dorsally by the light dorsolateral stripe.

Natural History. The type locality (Bosque de Cachil) is the site of a relictual patch of humid forest surrounded by degraded second growth and brushy, chapparral-like terrain (see Cadle and Chuna, 1995, for description). Specimens of *Stenocercus latebrosus* were observed only outside the limits of the humid forest along trails edged with secondary growth and in agricultural land. They were especially common around (and took refuge in) stone fences and rock walls, and in leaf litter along trails. Subadults and hatchlings were found under rocks on the ground. Similar-

ly, near Sinsicap *S. latebrosus* was collected along roads in relatively open degraded forest with eucalyptus and agaves. Field notes of Ray Hilborn and Carl B. Koford (MVZ field note archives) indicate habitats similar to these for the MVZ paratypes, including dry rocky and brushy hillsides mixed with agricultural land and planted eucalyptus. Fritts (1974: 61) reported (as *S. ornatissimus,* but in reality *S. latebrosus* as indicated above) that near Otuzco males "bask on rocks and *Agave,* whereas females frequently are at bases of shrubs and on the ground between rock patches." No other species of *Stenocercus* are known to be sympatric with *S. latebrosus,* but a species of the *Tropidurus occipitalis* group occurs in the vicinity of San Pablo, Cajamarca (personal observations).

On 17, 18 August 1994 both gravid females and hatchlings (SVLs 28–33 mm) were collected at Bosque de Cachil. All were active in full sun and took refuge in rock or debris piles or stone walls. Some individuals escaped by moving rapidly in leaf litter for a short distance and then remaining motionless in the open; these were well-camouflaged against the dry leaf litter. Cachil at this time was extremely dry (soil even under large boulders was dry and dusty). Days were hot but nights were very cool.

Remarks. Bosque de Cachil comprises a forest of approximately 100 ha in upper reaches of the Río Cascas basin, approximately 2,400–2,600 m elevation (Dillon, 1994; Dillon et al., 1995). The forest is dominated by *Podocarpus* and has abundant epiphytic mosses, bromeliads, and orchids. Floral and faunal surveys of this forest are incomplete, but another new species of lizard was described from the site (*Macropholidus ataktolepis* [Teiidae]; Cadle and Chuna, 1995) and several endemic plants are known (Dillon, 1994). Bosque de Cachil represents the southern terminus for many Pacific slope plant species, and the floral community is a mixture of moist forest elements from farther north and east and semiarid elements from farther south on the Pacific slopes (Dillon et al., 1995)

The coloration and meristic differences between the northern and southern samples of *Stenocercus latebrosus* (See *Sexual Dimorphism and Geographic Variation*) suggest that the the Río Chicama may represent a significant influence on differentiation of organisms in this region of the Andes. Unfortunately, far more survey work has been conducted north of the Río Chicama than south of it in the Cordillera Occidental, so that thorough analysis of this hypothesis is not presently possible. However, it is worth noting that the Río Chicama is the southern limit of at least four species of birds of the western Andean slopes (Francke, 1992), and the spur of the Andes delimited on the north by the Río Chicama harbors two endemic species of frogs (*Telmatobius* [Leptodactylidae]; Wiens, 1993).

Discussion: Comparison of *Stenocercus latebrosus* and *Stenocercus ornatissimus*

Most museum specimens of *Stenocercus latebrosus* from previous collectors were identified in their respective collections as *S. ornatissimus.* Aside from a slightly lower average midbody scale count in *latebrosus* compared to *ornatissimus,* the two species are very similar in standard meristic features that distinguish species of *Stenocercus* (Table 1). However, *Stenocercus latebrosus* seems to attain a larger body size and appears to be more robust than *ornatissimus* (15 mm difference in maximum size; Table 1). Although subject to some variation, the posterior head scales of *latebrosus* are smaller and more irregular than those of *ornatissimus* (compare Fig. 7 and Girard [1858: fig. 2]). Both species possess distinct mite pockets underneath the antehumeral and oblique neck folds. Mite pockets on the neck are highly unusual characters in *Stenocercus.* Hereafter these are referred to as the antehumeral mite pocket and the oblique mite pocket, respectively. Hence, I compare these two

TABLE 3. DISTINGUISHING CHARACTERISTICS OF *STENOCERCUS LATEBROSUS*, NEW SPECIES, AND *STENOCERCUS ORNATISSIMUS* GIRARD.

	Stenocercus latebrosus new species	*Stenocercus ornatissimus* (Girard, 1857)
Scales covering exterior of neck mite pockets	Nearly as large as dorsal neck scales	Less than half size of dorsal neck scales
Granular scales lining neck mite pockets	Not visible on lateral surface of neck; obscured by scales on exterior surface of the neck folds	Visible on lateral surface of neck; not obscured by overlying mucronate neck scales
Size of neck pockets	Oblique pocket large, occupying more than half of area between ear and forelimb	Oblique pocket small, occupying much less than half of area between ear and forelimb
Throat pattern (adult males)	Either (1) bold black streaks or reticulations or (2) thick, anastomosed reticulations enclosing white spots	Small black spots on whitish ground color; occasionally fine reticulations
Ventral pattern on belly posterior to pectoral region and on ventral surfaces of limbs (adult males)	Whitish or dusky, without black spots or reticulations	Small black spots often cover entire venter, including limbs (usually at least some spots on pectoral region and anterior abdomen)
Hemipenis	Thick "girdle" on asulcate surface below the lobes; flounces well developed at base of lobes	Asulcate "girdle" absent; flounces poorly developed

species in greater detail. Their distinguishing characters are summarized in Table 3.

Characters of the Mite Pockets Underneath Neck Folds (Fig. 12). In adult males of *Stenocercus latebrosus* and *S. ornatissimus* the antehumeral and oblique pockets are deep and internally lined with small granular scales (peripherally) and bare skin (deeply). In females the pockets are less extensive and sometimes are completely lined with scales (lacking bare skin). The following comparisons refer primarily to the structure of the pockets in adult males, although differences between the species are evident in females as well.

In *Stenocercus latebrosus* the scales covering the exterior of the oblique pockets are large, keeled, and mucronate. They completely obscure the granular scales underneath and project posteriorly to overlap the scales covering the antehumeral pocket. The covering is so extensive that it may be easy to overlook the fact that deep pockets reside underneath the scale coverings. On the other hand, in *S. ornatissimus* the exterior scales covering the oblique pockets are much smaller and keeled, but only slightly mucronate, not obscuring the granular scales underneath and not overlapping the scales covering the antehumeral fold (Fig. 12). The openings to the neck mite pockets in *S. ornatissimus* are superficially evident because of the reduced scale covering on the neck folds. The size contrast between the scales covering the neck mite pockets in the two species is evident by comparing these scales with the scales dorsolaterally on the neck: in *S. latebrosus* the largest scales covering the oblique neck pocket are only slightly smaller than the dorsolateral neck scales, whereas in *S. ornatissimus* the largest oblique neck scales are much less than half the size of the dorsolateral neck scales (Fig. 12).[5]

[5] An exception to this generalization is the male *Stenocercus latebrosus* from the Amazonian versant (MCZ 154240), in which scales covering the oblique neck fold are about half the size of the dorsolateral neck scales. Whether this is representative of eastern populations is not known. The neck pockets in MCZ 154240 do not appear as deep as in other specimens, but it was overinflated upon preservation and the appearance may be an artifact. In all other respects, including the distinctive throat pattern and observable hemipenial characters (see text), MCZ 154240 is

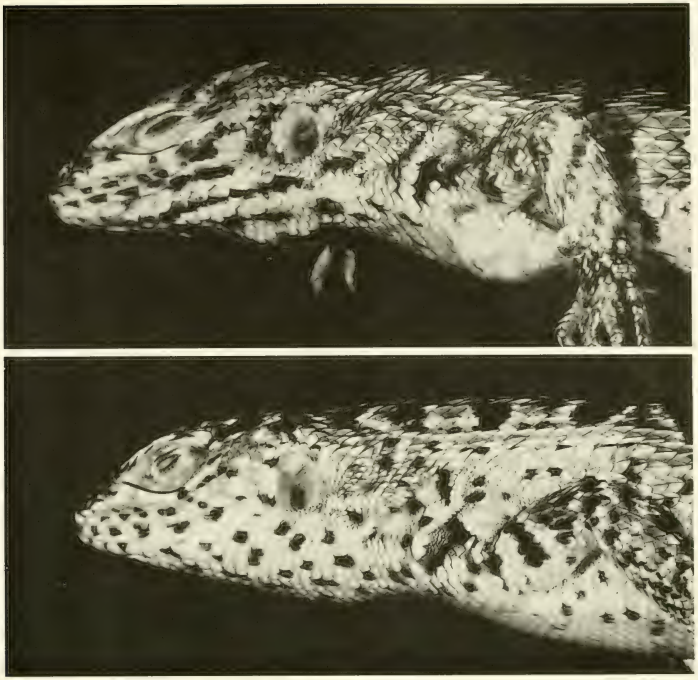

Figure 12. Comparison of scales on the side of the neck in *Stenocercus latebrosus* and *Stenocercus ornatissimus*. In *S. latebrosus* (top; MUSM-JEC 13027) the scales covering the exterior of the oblique neck mite pocket are large and obscure the underlying granular scales lining the edge of the pocket. In *S. ornatissimus* (bottom; MCZ 182154) the scales covering the exterior of the oblique neck mite pocket are smaller and do not obscure the underlying granular scales. A similar contrast is evident in the scales associated with the antehumeral mite pockets. Note also the throat patterns, consisting of dark lines in this specimen of *S. latebrosus* and dots in *S. ornatissimus* (see text and Table 3).

The sizes of the pockets also differ between *Stenocercus labebrosus* and *S. ornatissimus*. In *latebrosus* the oblique pocket is very large, occupying well more than half the space on the lateral surface of the neck between the posterior border of the ear and the insertion of the forelimb. In *ornatissimus* the oblique pocket occupies much less than half of this area. The antehumeral pockets are approximately equally developed in *latebrosus* and *ornatissimus*, but the smaller size of the latter gives the impression that the antehumeral pockets of *ornatissimus* are rather larger than those of *latebrosus*.

Ventral Color Pattern of Adult Males (Figs. 9, 24, 25). In adult males of *S. latebrosus* the throat has one of two patterns: bold black streaks or reticulations on a dirty white or dusky ground color or thick anastomosed reticulations enclosing large whitish spots. Dark spots or streaks, when present, are large and cover multiple scales. Black streaks and spots are confined

like other specimens of *latebrosus*. Several females from Sinsicap (e.g., MCZ 182244, MUSM-JEC 13839) also have small scales covering the oblique pocket, but other females from this population are typical in having large scales.

to the throat and pectoral region (absent from belly and limbs). In *S. ornatissimus* the typical throat pattern consists of small black spots on a whitish ground color. Each black spot usually covers only a single scale, although adjacent scales may be covered or the spots may anastomose to form longitudinal streaks (Fig. 25) or reticulations (e.g., FMNH 41559). In the latter case, the reticulations are always much finer than in *latebrosus*. In *S. ornatissimus* small black spots sometimes cover the entire venter, including the limbs, and there are usually at least scattered black spots on the pectoral region and anterior belly in addition to the throat (Fig. 24). In *S. latebrosus* there are often black longitudinal streaks present on the postmental series of scales, highlighting the whitish or spotted infralabials; these are absent in *S. ornatissimus* (Figs. 8, 12).

Hemipenial Morphology. Detailed comparison of the hemipenes of *Stenocercus latebrosus* (cf. above description and Fig. 11) and *S. ornatissimus* has not been possible because only a partially everted and somewhat damaged organ of *ornatissimus* (as here conceived) has been available (MCZ 182149). However, this hemipenis is different from that of *S. latebrosus* in two distinctive ways (see Fig. 11 and the description of *latebrosus*): (1) it lacks a thick "girdle" on the asulcate surface and (2) it entirely lacks or has only very poorly developed flounces at the base of the lobes; the calyces on the lobes in *ornatissimus* appear to extend to the base of the lobes on the sulcate surface. Like the hemipenis of *S. latebrosus* but unlike that of *S. stigmosus*, new species, described next, the calyces of the hemipenis of *S. ornatissimus* appear to be spinulate.

Remarks. The consistent differences between near-topotypic *Stenocercus ornatissimus* and northern populations from La Libertad and Cajamarca departments (Peru) previously assigned to that species (Fritts, 1974) make it virtually certain that distinct species are represented. Moreover, that such disjunct populations represent a single species (Fig. 1, distributions of *ornatissimus* and *latebrosus*) would be highly unusual for Andean species of *Stenocercus*. Most species of the Andes seem to have rather small ranges, often restricted to single valleys or habitat types (a distribution pattern that contrasts with many lowland species; Cadle, 1991).

Stenocercus stigmosus
new species
Figures 13–18; Table 1

Holotype (Fig. 13). **Museo de Historia Natural de San Marcos (MUSM)-JEC 10243**. **PERU: CAJAMARCA:** [Forest at] El Pargo, 8 km by road (Llama to Huambos) N of La Colmena, then 3–4 km NW by trail, 2,950 m [06°28′S, 79°03′W]. Adult male collected 18 September 1991 by John E. Cadle.

The type locality is in remnants of high montane forests that cover the crest of the continental divide between Llama and Huambos. El Pargo (Pargo on some maps) is a small settlement on the Amazonian versant that consisted (in 1991–1994) of two houses on the main road between Llama and Huambos.

Paratypes. **PERU: CAJAMARCA:** Same data as the holotype, **MCZ 182232–33**. 2–3 km (airline) NW El Pargo (Llama–Huambos road), 3,000–3,100 m [same locality as the type locality, differently stated], **MUSM-JEC 12923–24, 12927, 13000**, **MCZ 182234–35** (12–15 August 1994, J. E. Cadle, P. Chuna, and S. Leiva). 2 km SE Cutervo, 8,300 ft. [2,530 m; 06°22′S, 78°51′W], **LSUMNS 39477** (19 June 1978, G. R. Graves).

Referred Specimens. MUSM-JEC 10246–47 (hatchlings), same data as the holotype.

Distribution (Fig. 1). Known only from the highlands of central Cajamarca department, Peru. The dry rain-shadow valley of the Río Chotano separates the two known localities, so the species may be broadly distributed in the region. The forest at the type locality straddles the continental divide, whereas the Cutervo local-

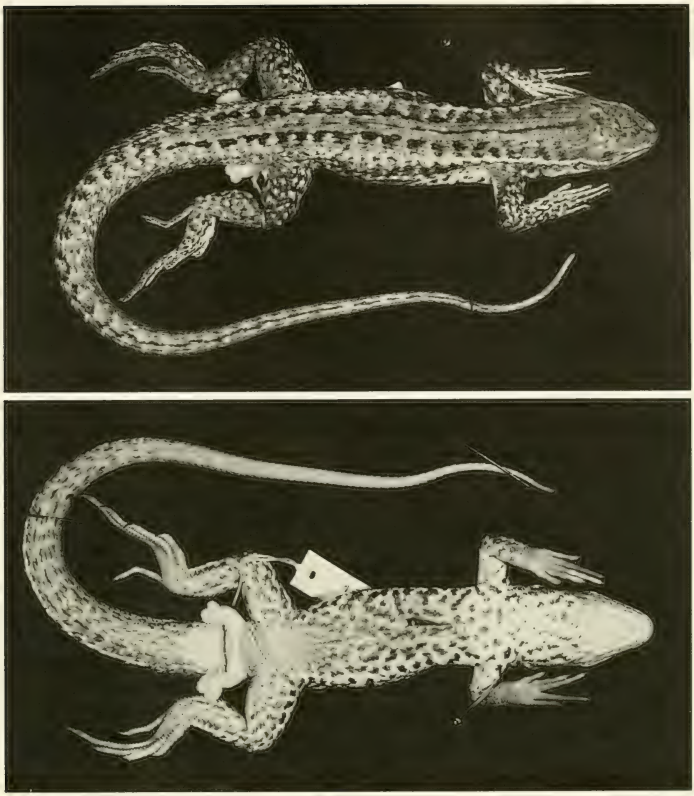

Figure 13. Holotype of *Stenocercus stigmosus* (MUSM-JEC 10243; adult male, SVL 64 mm). Dorsal and ventral views. The ventral spotting of males is diagnostic of the species.

ity is in the upper Marañon (Amazonian) drainage. The known elevational range is approximately 2,500–3,100 m.

Etymology. The specific epithet *stigmosus* is a Latin adjective meaning "full of marks," referring to the strongly patterned venter of adult males (Fig. 13).

Data on the Holotype. Adult male with everted hemipenes, midventral longitudinal slit in abdomen. SVL, 64 mm. Tail length, 132 mm. Total length, 196 mm. Tail as a percentage of total length, 67%. Midbody scales, 52. Gular scales between the ears, 25. Internasals, 3. Subdigitals on fourth fingers and toes, 18-18, 26-26, respectively.

Definition. A species of *Stenocercus* characterized by the following features (Fig. 14): (1) dorsal head scales smooth, juxtaposed, slightly protuberant. (2) No distinct parietals, postparietals, or occipitals; posterior head scales small; interparietal small, irregular, indicated by visible parietal eye. (3) Internasals usually 4. (4) Several supraoculars in a median row slightly enlarged. (5) Two canthals on ei-

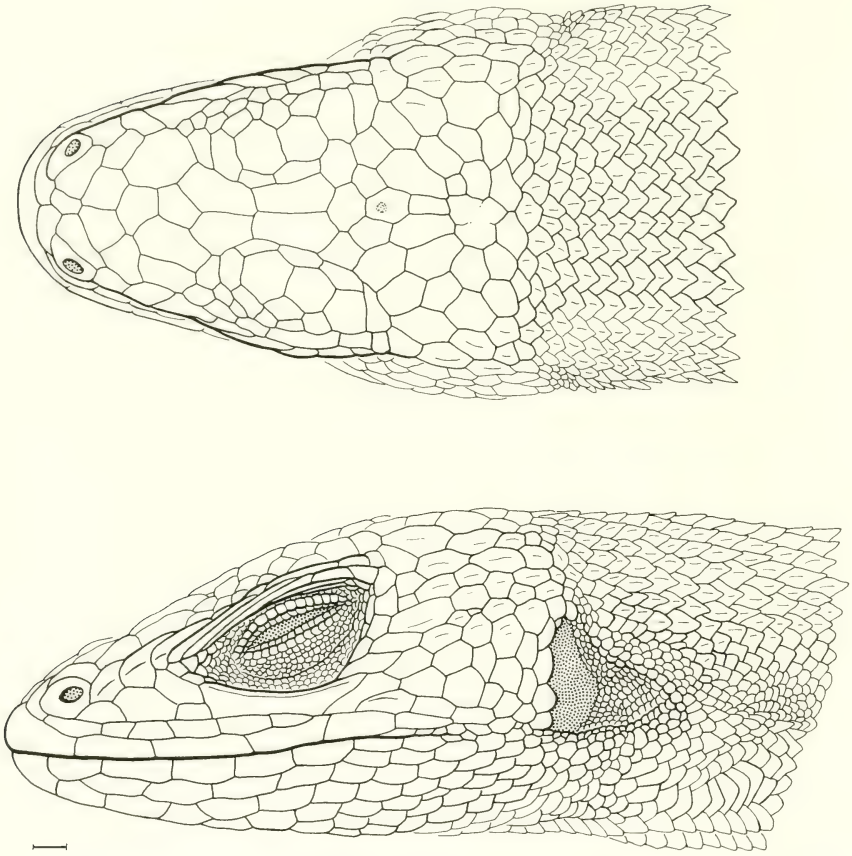

Figure 14. *Stenocercus stigmosus* (holotype, MUSM-JEC 10243). Dorsal and lateral views of head scales. Bar = 1 mm.

ther side between the superciliaries and the postnasals. (6) No projecting blade-like angulate temporals; scales in dorsal temporal region small and keeled. (7) Gulars and postmental series smooth. (8) Parietal eye distinct. (9) Neck folds weakly developed, consisting of antegular, oblique, longitudinal, and supra-auricular folds (see Cadle, 1991: fig. 1). (10) Dorsal scales imbricate, mucronate, and strongly keeled. (11) Vertebral row continuous, not strongly differentiated from paradorsal rows, and not bearing a projecting crest. (12) No posthumeral pocket (Type 1); a shallow postfemoral pocket (Type 3). (13) Scales of posterior thigh granular. (14) Tail somewhat compressed, more or less squarish at base. (15) Dorsal ground color of males brown with darker brown or black irregular or triangular markings in dorsolateral

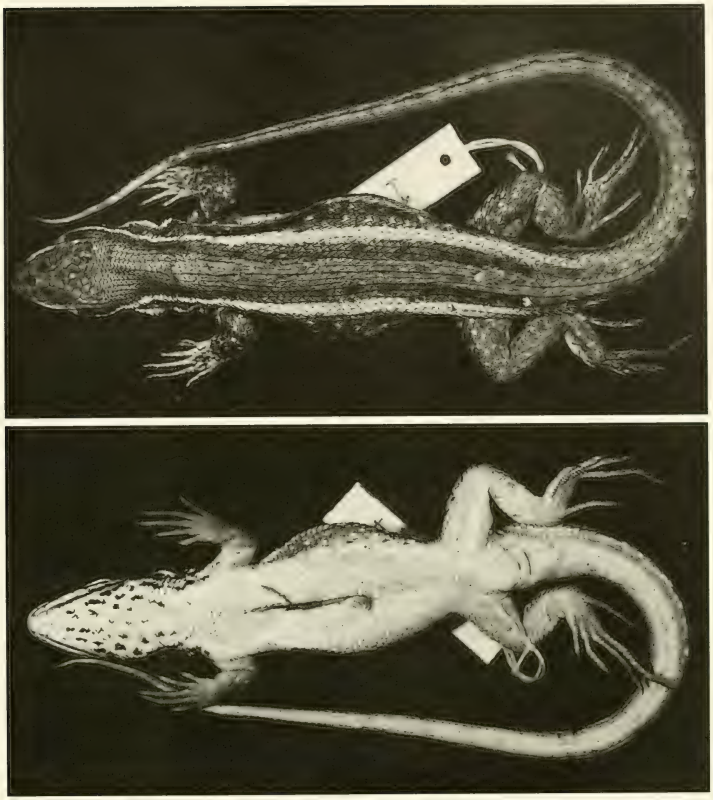

Figure 15. *Stenocercus stigmosus* (MCZ 182232; adult female, SVL 59 mm). Dorsal and ventral views showing pattern (compare Fig. 13).

and lateral series; venter of males, including throat, belly, limbs, and tail, with bold black spots and reticulations (Figs. 13, 16). Females brown dorsally, with light dorsolateral and lateral stripes; venter with black streaking and spotting on throat, otherwise dirty whitish, unmarked (Fig. 15).

Diagnosis. No other species of *Stenocercus* has bold black spots covering the entire venter, including limbs and tail, in adult males (Fig. 13). However, males in some southern populations referred to *S. chrysopygus* have black coloration on the ventral pelvic region and base of the tail, occasionally covering more of the venter (Fritts, 1974). *Stenocercus stigmosus* is very similar to *S. chrysopygus* in all meristic and mensural features (Table 1), and it will key to *S. chrysopygus* using Fritts' (1974) key. Fritts (1974) reported geographic variation in coloration and meristic features among populations of *S. chrysopygus.* However, topotypic males of *chrysopygus* (Río Santa valley, Ancash depart-

ment: Caraz, Huaraz, and Recuay; Fig. 1) invariably lack black ventral coloration except for occasional dark reticulations on the gular region (see *Specimens Examined*). In available males of *stigmosus* the black spots do not anastomose on the gular region to form reticulations, but maintain their distinctness. Furthermore, those populations of *chrysopygus* in which the venter of males has extensive black pigment are the most southerly populations—those farthest from the known localities for *stigmosus* (Fig. 1).

Females of *stigmosus* have a pair of light stripes on either side of the body from the eye to the base of the tail (dorsolateral stripe) or inguinal region (lateral stripe). Females of *chrysopygus* have light dorsolateral stripes but lack lateral stripes. Finally, the antehumeral neck fold in both sexes of *chrysopygus* is more strongly developed than in *stigmosus*, and in *chrysopygus* a distinct mite pocket, consisting of a scaleless patch of skin, is often present underneath the antehumeral fold. Such a pocket is lacking in *stigmosus*.

Aside from the distinctive male coloration, *Stenocercus stigmosus* can be distinguished from other species of *Stenocercus* by the combination of (1) no posthumeral pocket; (2) moderately developed postfemoral pocket (Type 3); (3) smooth dorsal head scales and ventral scales; (4) granular scales posterior to tympanum; (5) relatively low number of midbody scales (49–57; Table 1); (6) neck folds consisting of moderately developed antehumeral, oblique, and supra-auricular folds, but other neck folds absent; (7) no mite pockets underneath neck folds; (8) no projecting vertebral crest; and (9) no strongly spinose scales on the tail.

Stenocercus latebrosus and *S. ornatissimus* are similar to *S. stigmosus* in scutellational features (but not coloration), but they lack postfemoral mite pockets and possess mite pockets underneath the antehumeral and oblique neck folds. Other species in northern Peru and Ecuador have other combinations of characters, such as more midbody scales and/or spinose tails (*boettgeri, carrioni, chlorostictus, crassicaudatus, empetrus, eunetopsis, simonsi*), projecting dorsal crests (*festae, formosus, guentheri, huancabambae, humeralis, imitator, nigromaculatus, nubicola, ornatus, percultus, rhodomelas, variabilis*), keeled head scales (*ivitus, orientalis*), keeled ventrals and large posterior head scales (species of *Ophryoessoides sensu* Fritts, 1974), or imbricate post-auricular scales and well-developed gular folds (*cupreus*).

Description. Head. Dorsal head scales small, juxtaposed, smooth, and somewhat protuberant (Fig. 14). Parietal region with many small scales. Rostral large, in contact with first supralabial, first lorilabials, and 2 or 3 postrostrals. Two canthals anterior to the superciliary series, the anterior ones in contact with the nasals. Generally 4 elongate superciliaries overlapping posteriorly, followed by 2 shorter posterior superciliaries overlapping in the reverse direction. Internasals usually 4 (occasionally 3, rarely 2). Three or 4 median supraoculars enlarged. Parietal, postparietals, and occipitals not distinguishable; posterior head scales small, fragmented. Interparietal distinguished by a distinct parietal eye visible in all specimens. Lateral temporal scales juxtaposed, smooth except for the dorsal ones in the series, which are keeled. Gulars smooth. Mental in contact with first pair of postmentals and first pair of infralabials. Enlarged postmentals 3 or 4 on each side.

Neck and Body. Dorsal scales of neck, body, and tail imbricate, mucronate, and strongly keeled; on body grading abruptly into smooth, imbricate, and less mucronate ventrolateral and ventral scales. Preauricular fringe poorly developed, consisting of 3 or 4 scales. Scales immediately posterior to ear granular, grading into small subimbricate scales on side of neck. Scales in axillary region and immediately dorsal to forelimb insertion granular. Lateral neck scales much smaller than dorsal neck scales; more or less abrupt transition

between dorsal and lateral scales along the supra-auricular fold.

Vertebral crest absent; although the vertebral row may appear slightly more strongly keeled than other dorsal rows, this appears to be due more to the differentially black pigmented keels on this row than to any difference in keel size or projection. Ventral body scales (gulars, venter, limbs) smooth. Ventral scales approximately equal in size to dorsal scales.

Neck Folds. Skin of neck weakly folded. Moderately developed oblique, antehumeral, and longitudinal folds, and weakly developed supra-auricular folds are universally present. Other neck folds lacking.

Tail. Dorsal scales of tail strongly keeled, mucronate, and imbricate. Ventral scales imbricate, smooth at the tail base and weakly keeled distally. Tail slightly compressed.

Limbs. Dorsal and ventral scales of forelimbs moderately keeled. Dorsal scales of hindlimbs strongly keeled, ventral scales smooth. Scales on posterior surfaces of thighs granular. Supradigitals of forelimbs smooth, of hindlimbs keeled. Subdigitals multicarinate. Plantar and palmar scales strongly unicarinate.

Posthumeral and Postfemoral Mite Pockets. Posthumeral and postfemoral mite pockets Types 1 and 3, respectively. Posthumeral scales are granular, pavement-like. Postfemoral pocket located posterodorsally at junction of thigh and body, consisting of a bare or weakly keratinized skin pocket with a thickened border.

Size and Proportions. Largest male (MUSM-JEC 13000), SVL 68 mm. Largest female (MCZ 182233), SVL 61 mm. Tail 64–67% of total length.

Coloration and Pattern in Life. Adult Males in Life (Figs. 13, 16, based on the holotype). Top of head and dorsum dark medium brown. Thin whitish stripe from posteroventral corner of eye to top of ear, continuing as an interrupted bright yellow dorsolateral stripe to the base of the tail (on the body manifested as a longitudinal series of yellow flecks). Medial to the yellow stripe, ground color is light brown, which is separated from middorsal brown color by a brownish black wavy border, giving medial edge a scalloped effect. Postauricular region and flanks brown, heavily flecked with yellow and dark brown. Elongate subocular and 1 or 2 presuboculars dull whitish. Canthals somewhat lighter brown than rest of head color.

All males have some indication, more or less marked in different individuals, of blackish irregular markings dorsolaterally from the neck to the tail base. These form pairs on either side that are well separated on the midline. Often the keels on many or most scales of the vertebral row are black, giving the appearance of a fine middorsal line.

Upper surfaces of limbs dark brown flecked with tan. Mental, postmentals, and anterior gulars dull whitish, some with brownish borders giving appearance of dark line between sublabials and postmentals. Posterior gulars (from the level of the jaw angle) and pectoral region pale yellow irregularly spotted with dark brown. Ventral fore- and hindlimbs similar, but yellow on hind limbs is a deep bright yellow. Belly between pectoral and inguinal regions bright green, irregularly spotted with dark brown. Dorsal tail similar to body but stripes indistinct (giving appearance of brown flecked with yellow and darker brown). Ventral tail dull yellowish at base, then greenish flecked with dark brown for nearly one-half of tail length, then fading to medium light brown, generally unflecked.

Adult Females in Life (Figs. 15, 17, based on MCZ 182232, a topotype). Top of head and middorsum medium brown. Pale tan dorsolateral stripe beginning at posteroventral corner of eye, over top of ear, and continuing onto base of tail. This stripe bordered above on body and tail by a somewhat wider reddish brown stripe. Dull white line from angle of jaw to scapular region, passing ventral to ear; here it is briefly interrupted, then continues as a less distinct light (pale tan) stripe to inguinal

Figure 16. Adult males of *Stenocercus stigmosus* in life from the type locality. *Top,* MCZ 182234. *Bottom,* MUSM-JEC 10243. Note the indistinct dorsolateral and lateral stripes, and the differences in dorsal and flank patterns in the two specimens.

region. On the head and neck this stripe is bordered ventrally by a black stripe. Flanks between lateral and dorsolateral light stripes brown flecked sparsely with pale tan. Scapular, suprascapular, and posthumeral region with yellow wash. Dorsal surface of limbs brown with a few lighter flecks. Flanks below lateral light stripe brown with lighter flecks and entire area with yellow wash. Throat and gular region dull white with dark brown small spots. Dark brown line between postmentals and sublabials widens to form broad dark brown area on side of neck to the base of the forelimb. Ventral surfaces of belly, limbs, and tail more or less homogeneous grayish tan/brown without markings.

Most females are very similar to that just described. The dorsolateral and ventrolateral stripes are constant features. Several adult females (e.g., MCZ 182233) had a very light rosy or coppery sheen on the belly and a yellow wash on the ventral surfaces of the hindlimbs. One female (MUSM-JEC 12923) had a bright rusty red color from the posteroventral corner of the eye to just behind the ear and extending below the ventrolateral stripe on the neck and anteriorly along the infralabials. This peculiar female coloration is indicative of a gravid condition in some oth-

Figure 17. Adult female of *Stenocercus stigmosus* in life from the type locality (MCZ 182232). Note the distinct dorsolateral and lateral stripes characteristic of females.

er tropidurids and in some phrynosomatid lizards, but not in this particular case: MUSM-JEC 12923 is a subadult female (SVL 48 mm).

Coloration in Preservative. All of the brilliant colors (yellows, greens, etc.) of the dorsum and venter are lost in preservative. Dark brown appears blackish in preservative. Preserved lizards are basically brown dorsally and dirty whitish ventrally, with bold black markings dorsally and ventrally.

Figure 18. Hemipenis of *Stenocercus stigmosus* (MUSM-JEC 12924) in "lateral" view. Sulcate surface is to the left, asulcate to the right; proximal toward the bottom. The tips of the lobes are slightly uneverted, and would probably have much the same form as the hemipenis of *S. latebrosus* (Fig. 11). The broad, thick flounces at the base of the lobes on the sulcate surface are visible (compare *S. latebrosus*, Fig. 11), as are the calyces covering the lobes.

Scale Counts and Qualitative Characters (Table 1). The scale counts are moderately high, indicating the smaller scales of this species compared, for example, with *Stenocercus latebrosus.*

Hemipenis (Fig. 18). An everted hemipenis of *Stenocercus stigmosus* from the type locality was examined (MUSM-JEC 12924). The organ is about one-third bilobed. The sulcus spermaticus divides at the separation of the lobes. Each branch passes a short distance along the crotch side of the lobe (centripetally), then passes to the outer side of the lobe and appears to end just short of the tip of the lobe. The lobes are broad at the base and taper to points. The tips of the lobes of this specimen are slightly uneverted and would probably have a form similar to that of *S. latebrosus* (Fig. 11) if completely everted.

The base of each lobe on the sulcate side is ornamented with broad, overlapping flounces. These pass to the asulcate side just proximal to the lobes, where about 5 to 6 flounces encircle the organ. Adjacent flounces are occasionally connected by ridges of tissue, forming incipient calyces. Distally on each lobe the flounces are rather abruptly transformed

into calyces by augmentation and accentuation of these connecting ridges. Both the flounces and the walls of the calyces on the hemipenis of *Stenocercus stigmosus* are much thicker than those of *S. latebrosus* and the calyces in *stigmosus* lack surmounting spinules. The crotch of the organ is nude and the calyculate areas are well separated. However, the flounces form a prominent and continuous band around the hemipenis below the lobes. The basal undivided portion of the organ has several irregularly placed transverse folds that are similar to the flounces, except that they are formed of much thinner tissue and are not broad like the well-developed distal flounces.

Sexual Dimorphism and Geographic Variation. Males attain a slightly larger size than females (Table 1) and differ in coloration and pattern (see above). Females have quite distinct dorsolateral and lateral light stripes, whereas in males usually only the dorsolateral stripe is distinct. The sexes do not differ significantly in standard scale counts. The male from near Cutervo (LSUMNS 39477) has fewer subdigital scales on the fourth finger than the topotypes (14 vs. 17–19), but otherwise does not differ in substantive ways from them. This seems rather remarkable in view of the the considerable physiographic fragmentation in this portion of the Andes and the separation of the two localities by the broad dry valley of the Río Chotano.

Natural History. The type locality for *Stenocercus stigmosus,* the forest at El Pargo, was the site of a transect sample for plant diversity by the late Alwyn H. Gentry, who classified the forest as "humid montane forest" according to the Holdridge (1967) system and estimated the precipitation at 1,200 mm annually (Gentry 1992, 1995). I visited the site in September 1991 (with Gentry) and in August 1994. The following comments are taken primarily from my field notes of 8 September 1991. The forest, located at the crest of the ridge on the continental divide along the road between Llama and Huambos, is a high montane cloud forest dominated by *Weinmannia* and *Oreopanax* (Figs. 19, 20). El Pargo itself is a couple of dwellings on the main road at 2,790 m. From there a trail ascends to the forest, which begins at about 2,900 m and locally extends to just over 3,000 m. Between the road and the forest the trail crosses a large area of chaparral-like vegetation with grayish white, claylike soil; this area is heavily disturbed by cattle grazing and frequent burns. Apparently, the area has very few natural streams, but there is an extensive array of irrigation ditches constructed by locals. The forest itself has a very dense understory and the trees are festooned with epiphytes (bromeliads, orchids, mosses, etc.).

The forest at El Pargo is presently a rather small isolated patch but may once have been much more extensive, as suggested by large areas adjacent to the present forest with felled logs and standing trunks (Fig. 21). Additional forest remnants that were probably continuous with it were still present in 1994 at higher elevations on the ridge forming the western edge of the Río Chotano valley, which is accessible via a road passing north to Querocoto and Querocotillo. However, these forests are probably doomed. Many patches had been cut from the forest at El Pargo in 1991, and these were in various stages of second growth or were converted to cattle pasture (Fig. 21). In 1994 additional portions had been cut, and there was active felling of trees using chain saws. Likewise, most of the forest near the road in the Río Chotano valley is heavily disturbed and subject to continued destruction.

On 18 September 1991 at El Pargo, I collected two hatchlings (MUSM-JEC 10246–47; SVLs 28 and 24 mm, respectively), two adult females, and one adult male *Stenocercus stigmosus* from brush piles in and around a recently cleared field surrounded by forest. The adult females (MCZ 182232–33) contained enlarged shelled eggs. The lizards took refuge in

Figure 19. Forest at the type locality of *Stenocercus stigmosus*. *Top* (photographed 12–15 August 1994), overview of the continental divide showing dense forest blanketing the slopes. Slopes to the right are east of the continental divide (Amazonian drainage), whereas those in the background are west of the divide (Pacific drainage). The crest of the divide is somewhat over 3,000 m elevation. *Bottom* (photographed 8 September 1991), closer view of the forest. The dense clouds in the background were characteristic during visits to El Pargo in August and September.

Figure 20. A trail through the forest at El Pargo (photographed 8 September 1991). The dense shrubs in the foreground are a product of the light gap created by the trail but the dense trees are characteristic of this forest (see also Figs. 19, 21).

brush piles and undergrowth. The day was cloudy and cool, and no active lizards were seen.

On 13–15 August 1994, 0900–1300 hr at the same locality, I collected a series from trail edges, mostly in secondary growth under piles of debris (decaying logs, etc.). The lizards were more evident in 1994 than in 1991, probably due to the warm sunny days in 1994 versus cloudy and cool days in 1991. As in 1991, *Stenocercus stigmosus* was mostly terrestrial (heard more often than seen, skittering through leaf litter at trailside) but was occasionally observed on or in stone fences in the area. Retreat sites at night or after being disturbed when active were underneath logs or piles of debris. The only other natural history data for *Stenocercus stigmosus* are on the specimen tag for LSUMNS 39477, indicating that the specimen was collected in "dense grass and shrubs on a mountain slope."

Stenocercus stigmosus is not known to be sympatric with other species of *Stenocercus*, although both *S. eunetopsis* and *S. crassicaudatus* are known from slightly lower elevations (<2,700 m) near the type locality (personal observations). The only other lizard known from the type locality is *Proctoporus ventrimaculatus* (Teiidae).

DESCRIPTIVE NOTES AND COMMENTS ON *STENOCERCUS ORNATISSIMUS* (GIRARD)

Girard (1857, 1858) described *Saccodeira ornatissima* on the basis of specimens from "Obrajillo and Yanga, Peru" obtained by the U.S. Exploring Expedition. Richard Etheridge (in Peters and Donoso-Barros, 1970) first associated the species with *Stenocercus*. The U.S. Exploring Expedition used Callao (Lima) as a base from June–November 1839 (Jackson, 1985), and the types of *S. ornatissimus* were collected during that time.

Stenocercus ornatissimus has remained poorly known since its description, and I have no field experience with it. As reported above, Fritts' (1974) discussion of

Figure 21. Forest destruction at El Pargo (both photographed 8 September 1991). *Top,* a recently cut and burned patch of forest destined for agricultural use. *Bottom,* the older cut area immediately peripheral to the existing forest, which is visible in the right background. Note the numerous felled and standing logs, which indicate that the original extent of the forest was much greater. From right to left the people are botanists Roza Ortiz, Camilo Díaz, Alwyn H. Gentry, and two local inhabitants.

ornatissimus relied primarily on a series of *S. latebrosus* from near Otuzco in northwestern Peru (La Libertad department). My review of *ornatissimus* was largely in the context of diagnosing *latebrosus.* I consider *ornatissimus* to be restricted, as presently known, to Lima department, Peru (Fig. 1); although, as indicated in footnote 7 and the discussion below, the relationship to *ornatissimus* of certain populations currently referred to *Stenocercus chrysopygus* bears further scrutiny. The obser-

vations reported here are based on study of the existing type and specimens from near the type locality (see *Specimens Examined*). Scutellational data on these samples are reported in Table 1.

Type Material and Designation of Lectotype. The type series of *Stenocercus ornatissimus* consisted of a male from "the Lower Cordilleras, just below Obrajillo" [11°23′W, 76°41′W; Canta province, Lima department, 2,764 m elevation; Stiglich, 1922] and a female from "Yanga" [=Yangas, Canta province, Lima department, 3,106 m elevation].[9] The type localities are two nearby villages in mountains northeast of the city of Lima. The male specimen has not been located (apparently not at USNM or ANSP). The female is now USNM 5655 and it is hereby designated the lectotype (Fig. 22).

USNM 5655 is in fair condition and has the belly opened and the distal portion of the tail missing. The specimen is adult, evidenced by a large shelled egg in the body cavity (an additional egg was originally present, as indicated by a large vacuity in the abdomen). Originally described in brief format (Girard, 1857), *S. ornatissimus* was given a more extended description a year later (Girard, 1858). Additional details for USNM 5655 not provided by Girard are as follows: SVL 54 mm, proximal unbroken portion of tail 17 mm, 49 scales around midbody, 2 canthals, 4 internasals, 19-18 subdigitals on the fourth fingers, 28?-29 subdigitals on the fourth toes. Few details of the pattern remain on USNM 5655, but Girard (1858) described the coloration of the male syntype in detail and gave more cursory notes on the female.

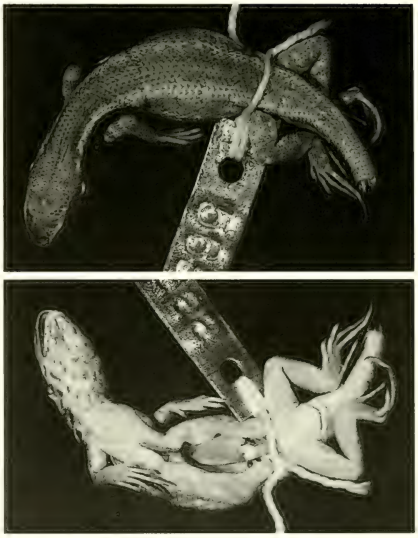

Figure 22. Lectotype of *Stenocercus ornatissimus* (Girard) in dorsal and ventral views. (USNM 5655; female, SVL 54 mm).

Diagnosis and Descriptive Comments. Because Girard's (1857, 1858) descriptions are excellent, I provide only a summary diagnosis of *Stenocercus ornatissimus* to distinguish it from species subsequently described. The most distinctive feature of *S. ornatissimus,* a pair of mite pockets on each side underneath the antehumeral and oblique neck folds, formed the basis of Girard's generic name *Saccodeira* (from Greek *sakkos* = bag or pocket, and *deire* = neck). This character distinguishes *S. ornatissimus* from all species of *Stenocercus* except *S. latebrosus* described herein; characters distinguishing these two species and details on the mite pockets of *ornatissimus* are given in the discussion of *latebrosus* (see Fig. 12; Table 3). Although a few other species of *Stenocercus* occasionally have mite pockets underneath the antehumeral folds (Cadle 1991: 82), they are not as fully or consistently developed as in

[9] This "Yangas" is in Arahuay district according to Stiglich (1922), who gave the elevation reported here; it is not on the maps or in the gazetteers consulted. The town of Arahuay (and thus Yangas, approximately) is at 11°37′S, 76°40′W. This locality should not be confused with the large town of Yangas on the Río Chillon northeast of Lima (11°41′S, 76°41′W), which is indicated on most maps; it is well below 1,000 m elevation. My determination of Girard's "Yanga" is based on the elevation, its nearness to Obrajillo, the other type locality, and other definite localities for this species, all of which are above 2,000 m elevation.

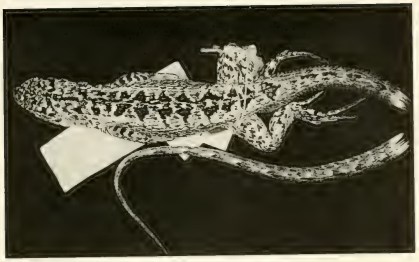

Figure 23. Characteristic dorsal pattern of *Stenocercus ornatissimus* (MCZ 182154, adult male). All recently collected specimens of both sexes which were examined have paired series of triangular blotches on the dorsum.

Figure 24. Characteristic ventral pattern in adult males of *Stenocercus ornatissimus* (MCZ 182154 and 182150, top and bottom, respectively). Small spots are invariably present on the throat and anterior pectoral region, as in MCZ 182154. In other specimens the spots are much more extensive, covering the entire venter, limbs, and tail, as in MCZ 182150. In females spots are less distinct and usually restricted to the throat and anterior pectoral region (Fig. 25).

S. ornatissimus and *S. latebrosus*, the single exception being some populations of *Stenocercus "chrysopygus"* that have deep pockets under the antehumeral fold (see footnote 7 and discussion below). Distinct mite pockets underneath the oblique neck folds are unknown in *Stenocercus* aside from *ornatissimus* and *latebrosus*.

Girard (1857, 1858) described the head scales of *Stenocercus ornatissimus* as subtuberculous or moderately multicarinated. In USNM 5655 and most specimens I have examined, the head plates are smooth. Distinct keeling, when present, is mostly restricted to lateral scales in the occipital region. Several specimens have decidedly tuberculate or wrinkled head scales (e.g., MCZ 182149–50, FMNH 41559 [126, 130]), in which case the posterior head scales and supraoculars are most often involved.

Girard's (1858: 325, 326) description of color pattern is accurate for all recent specimens I have examined (Figs. 23–25):

> A double series of blackish-brown, light-margined, subtriangular spots may be observed along the back, with their bases parallel to the dorsal line . . . . These spots or bands may be traced along the upper surface of the tail to its tip . . . . The chin, throat, and a portion of the chest are whitish, over which are interspersed small jet-black spots, of various shapes.

The extent of spotting on the venter in males varies (Figs. 24, 25). Small spots are universally present on the throat and pectoral region but may also occur over most of the venter, including limbs and tail (Fig. 24). In most specimens the throat spots are discrete and slightly irregular, but in other specimens adjacent spots fuse to form longitudinal streaks (Fig. 25). In some specimens (FMNH 41559) the streaks anastomose to form reticulations. Females have reduced spotting on the venter compared to males (Fig. 25). In females, the spots are nearly always restricted to the throat and are less prominent than in males.

Figure 25. Variation in throat patterns of adult *Stenocercus ornatissimus*. Far left, MCZ 182152, adult female. All others are adult males, left to right, MCZ 182153, 182154, 182149.

Distribution (Fig. 1). Stenocercus ornatissimus as here conceived is known from elevations of approximately 2,000–3,400 m on the Pacific Andean slopes of Lima department (approximately 11°20–12°S latitude).

STATUS OF *STENOCERCUS* POPULATIONS OF WESTERN ANCASH DEPARTMENT (PERU) AND THE PROBLEM OF VARIATION IN *STENOCERCUS CHRYSOPYGUS*

As pointed out in the discussion of *Stenocercus latebrosus* (footnote 7), the systematic status of some populations in western Ancash department, Peru, is in doubt. Their relationship to *S. chrysopygus, S. latebrosus,* and *S. ornatissimus* needs additional study. Verified literature references and specimens identified as *S. ornatissimus* from northern Peru (Ancash and La Libertad departments) have usually referred to either *S. latebrosus* or (more questionably) to *S. chrysopygus.* Nevertheless, the identity of samples from near Pariacoto and Marca in western Ancash is difficult to establish, as is the relationship of some other samples referred to *chrysopygus* from the eastern and southern part of its range (see *Specimens Examined*).

The Pariacoto and Marca populations are on the Pacific slope of the Andes and are separated from topotypic populations of *Stenocercus chrysopygus* by very high ranges (>4,000 m) of the Cordillera Negra. A gap of nearly 200 km separates Marca in southwestern Ancash from the nearest population of *S. ornatissimus* in Lima department from which I have examined specimens. The samples from Pariacoto and Marca differ from topotypic *chrysopygus* and *ornatissimus* in several characters. The antehumeral pockets are moderately to well developed in these populations, but they lack mite pockets under the oblique folds; in these respects they are like samples from east of the Cordillera Negra referred to *chrysopygus.* The Pariacoto/Marca specimens are similar to topotypic *ornatissimus* in having triangular blotches on the dorsum (compared to rectangular or irregular blotches in *chrysopygus*), but they have moderately developed postfemoral pockets (Types 2 and 3), which are absent in topotypic *ornatissimus.* In other respects, such as scale counts and patterns, they are similar to both *chrysopygus* and *ornatissimus.* One interpretation of the Pariacoto/Marca populations is that they represent the northern extension of *S. ornatissimus* on the Pacific versant, which is thus allopatric to *S. chrysopygus.* The differences between them and topotypic *ornatissimus* would then be viewed as geographic variation. On the other hand, a similar interpretation is possible vis-à-vis these populations and *chrysopygus.*

Further confusing the issue is the extensive variation among other populations currently referred to *S. chrysopygus* (footnote 7). Nonetheless, the type localities of *chrysopygus* are from high elevations in the interandean valley of the Río Santa, a major river flowing into the Pacific Ocean (Fig. 1). These populations are isolated from those of the Pacific versant in western Ancash by the aforementioned high range of the Cordillera Negra. Likewise, they are isolated from eastern and southern populations (Huánuco and Ancash departments) by the extensive high ranges of the Cordillera Blanca, the highest mountains in Peru (>5,000 m elevation and with some peaks >6,000 m). It would not be surprising to discover that this rugged terrain harbors more than one species similar to *chrysopygus* or that the isolating effect of the mountains produces extensive variation among populations within a single species.[10] A complex of closely similar species existing in the juncture of Ancash,

[10] The samples of *Stenocercus chrysopygus* studied herein extend its distribution to the east beyond that reported by Fritts (1974). LSUMNS 27243–44 are from the upper Río Huallaga drainage and separated from the next localities to the west by high mountains (>4,000 m) and by the upper Río Marañon valley.

Lima, and Huánuco departments is one possible interpretation consistent with the known variation exhibited by these populations. If this is true, then the limits and distributions of the species are currently confused.

Resolution of the status of the populations of western Ancash, as well as that of all populations of *Stenocercus chrysopygus* will require a more thorough study of geographic variation in *Stenocercus chrysopygus*. However, that may not be possible with existing museum collections. Additional samples from both sides of the Cordillera Negra and Cordillera Blanca will probably be needed. Additionally, field work in southern Ancash department and northern Lima department, especially on the Pacific versant, would provide samples relevant to assessing the relationship of these populations to *ornatissimus* to the south. This region seems to be relatively devoid of existing museum specimens of *Stenocercus*, a deficiency that hampers resolution of the current problem.

ACKNOWLEDGMENTS

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SPECIMENS EXAMINED

Institutional abbreviations are given in the *Materials and Methods*. Locality data from the respective museum catalogs and/or specimen tags are followed by bracketed information (usually elevations or coordinates) inferred from other sources (see *Materials and Methods*).

Stenocercus ornatissimus (Girard)

PERU: LIMA: Marcahuasi (Prov. Huarochiri, Distr. San Pedro de Casta)[approximately 11°46′S,

76°35′W], ANSP 31837–38. Matucana [2,378 m; 11°51′S, 76°24′W], FMNH 41559 (9 specimens, identified individually by field numbers). San Pedro de Casta, approximately 3,400 m [11°46′S, 76°35′W], MCZ 182148–54. Surco, 2,050 m [11°52′S, 76°28′W], BMNH 1901.8.2.57–58. Verrugas [a quebrada whose mouth is at 1,725 m elevation and 11°52′S, 76°29′W fide Lamas, 1976; empties into the Río Rimac], USNM 75398. Yanga [=Yangas, 3,106 m, approximately 11°37′W, 76°40′W; see footnote 9], USNM 5655 (lectotype).

Stenocercus chrysopygus Boulenger

PERU: Locality uncertain (?ANCASH): "near Chimbote", FMNH 5658–59 [specimens presumably from mountains E of Chimbote, which is a coastal city at sea level]. **ANCASH:** Carohas [coll. by P. O. Simons, whose 'Carohas' probably = Carhuás fide Stephens and Traylor (1983)] [2,625 m; 09°16′S, 77°38′W], MCZ 8073. Huaraz region [approximately 09°32′S, 77°32′W], AMNH 63475–76, MCZ 45833–34, 45836. Huaylas (Prov. Huaylas) [2,721 m; 08°52′S, 77°54′W], MCZ 157229–31. Tingo, 2 km S and 15 km W Huaras, 12,000 ft. [3,658 m; 09°31′S, 77°35′W], MVZ 82311. **[HUANUCO]:** Aguamiro, 11,500 ft. [3,506 m; 09°48′S, 76°48′W], FMNH 3546. Below Bosque Zapatagocha above Acomayo, ca. 7,600 ft. [2,317 m; approximately 09°46′S, 76°05′W], LSUMNS 27243. Base of Bosque Zapatagocha above Acomayo, ca. 8,400 ft. [2,561 m; approximately 09°46′S, 76°05′W], LSUMNS 27244.

Stenocercus ?chrysopygus

PERU: ANCASH: 1 km N and 12 km E Pariacoto, 8,500 ft. [2,591 m; 09°31′S, 77°45′W] MVZ 82308–10, 82346–50, 82393, 119232. 31 km (by road) E Pariacoto, 9,000 ft. [2,744 m; approximately 09°31′S, 77°40′W], LSUMNS 35236–39. Marca, 3,000 m [10°05′S, 77°30′W], BMNH 1900.6.20.20.

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NOTE ADDED IN PROOF: Jesús Cordova kindly provided MUSM catalog numbers for specimens referred to herein by "MUSM-JEC" field numbers. These are:

Stenocercus latebrosus:

JEC 10323 = MUSM 16743
JEC 13014 = MUSM 17107
JEC 13021 = MUSM 17108
JEC 13022 = MUSM 17109
JEC 13024 = MUSM 17110
JEC 13027 = MUSM 17111
JEC 13029 = MUSM 17112
JEC 13836 = MUSM 17103
JEC 13838 = MUSM 17104
JEC 13839 = MUSM 17105
JEC 13840 = MUSM 17106

Stenocercus stigmosus:

JEC 10243 = MUSM 17113 (Holotype)
JEC 12923 = MUSM 17114
JEC 12924 = MUSM 17115
JEC 12927 = MUSM 17116
JEC 13000 = MUSM 17117
JEC 10246 = MUSM 17118
JEC 10247 = MUSM 17119

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The Neotropical and Mexican Orb Weavers of the Genera *Cyclosa* and *Allocyclosa* (Araneae: Araneidae)

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THE NEOTROPICAL AND MEXICAN ORB WEAVERS OF THE GENERA *CYCLOSA* AND *ALLOCYCLOSA* (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. Fifty-one neotropical and Mexican species of *Cyclosa* were identified, of which 38 are new. Twelve names have been newly synonymized. The neotropical *Cyclosa* species all have genitalia similar to those of North American *C. caroli*, *C. turbinata* and *C. walckenaeri*. In all females, the epigynum is lightly sclerotized, with openings and sculpturing difficult to see. In most males, the diagnostic palpal features are hidden: the conductor tooth is behind a flap, and the median apophysis is partly hidden below the large conductor of the palpus. A new genus, *Allocyclosa*, has been established for *C. bifurca*. Synapomorphies place *Cyclosa* close to *Metazygia*, but *Allocyclosa* is similar to *Cyrtophora* in body shape. It differs from *Cyrtophora* in structure of genitalia and in making a *Cyclosa*-like web.

INTRODUCTION

This is one of a series of monographs on American orb weavers of the family Araneidae. Previous papers are listed in Levi (1993, 1996, 1997).

The *Cyclosa* species north of Mexico have been described and illustrated in Levi (1977). O. Pickard-Cambridge (1889–1902) and F. P.-Cambridge (1904) named and illustrated the Mexican and Central American *Cyclosa*, although the similarity of their genitalia make them difficult to separate. Of the 23 names for South American *Cyclosa* listed in the five catalogs for spiders (Roewer, 1942; Brignoli, 1983; Platnick, 1989, 1993, 1997), only three are easily recognized: the widespread North American species *C. caroli*; *C. bifurcata* (Walckenaer), separated from *C. walckenaeri* and redescribed and illustrated by Keyserling (1892–93); and *C. tri-quetra*, described by Simon (1895). Numerous new names added in this century did not recognize earlier descriptions. One of the remaining 20 South American names, *C. sericaria* Simon, is a nomen nudum, without description. Seven of the 20 species have been found to belong to other genera. The type of *C. tricolorata* Mello-Leitão is lost, and thus could not be recognized. The 11 species remaining have been identified and are illustrated here for the first time or their names are synonymized. Eight of these 11 were described from Guyana, from which few collections were available. There may be specimens from Guyana in the Natural History Museum, London, but the undetermined collection was not available for loan.

METHODS AND ACKNOWLEDGMENTS

The methods used are described in Levi (1993). To overcome the difficulties in studying the thin transparent epigyna of *Cyclosa* species, the specimens were examined in alcohol, resting on a background made of short strips of black Velcro® glued into a glass dish or in a dish with black silicon carbide crystals as background.

The ventral surfaces of the epigyna face slightly anteriorly and are illustrated from a slightly anterior position. The posterior surfaces face ventrally and are illustrated from a slightly ventral position. To increase visibility of the sculpturing of the epigynum, some specimens were temporarily dried. Ventral surfaces of other females were stained with drops of household dyes, such as tincture of iodine and textile

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

dyes. These dyes washed out rapidly, and did not leave the specimen stained. Although drawings were made of the vulva and other internal structures of the epigynum, as in all araneids their internal genitalia are similar and the ducts soft and difficult to see. If more permanent biological stains could be used, then destained, the loops of the internal ducts would be visible from the outside; however this method would damage specimens.

Species matching of males with females is more difficult in *Cyclosa* than in other araneid genera. Not only are the two sexes infrequently collected together, but they look so different that often they are separated into different genera when incoming collections are sorted.

The palpi of a few specimens were expanded in hot 10% sodium hydroxide and then transferred into distilled water. Ultrasonic vibration of the palpus in ethanol removed the embolus from its enclosure in the gutter of the conductor.

Scanning electron micrographs would have been useful for study of the surface of the epigyna and for the small male palpi, but no funds were available for this.

In descriptions, the distances between eyes of the anterior row are expressed as diameters of the anterior median eyes (in profile); distances between eyes of the posterior row are given as diameters of the posterior median eyes (in profile). The height of the clypeus (the distance from the anterior median eyes to the edge of the carapace), is expressed in diameters of the anterior median eye (Levi, 1993, fig. 28f).

Eyes of *Allocyclosa* and *Cyclosa* were examined by removing the entire eye region from the cephalothorax and placing it in alcohol. Tissues around the eyes were removed with needles. After being removed from alcohol and blotted with tissue, the eye region was immersed in methyl benzoate, which clears the eyes except for the tapetum. In *Allocyclosa*, black pigment hid cell rows, so the eye region was returned to alcohol, then to water, and then to a dilute mixture of Clorox® (sodium hypochlorite) for five minutes before being returned to methyl benzoate for re-examination.

Measurements of the ratio of femur and corresponding patella and tibia may have been made from a different specimen than the rest of the description. The design of the microscopic reticule allows for greater accuracy in measurements of small specimens than of large ones. Seven different females of *C. merretes* were measured to assure that their fourth femur is always as long or longer than the corresponding patella and tibia.

Carapace overhang makes the length of the carapace difficult to measure, so size ratio of male to female was obtained by measuring carapace width instead. Abdomen and total length are always smaller in the male than in the female, but the legs of males may be longer. Minute males, as in *Allocyclosa* and some other araneid genera, lack the endite tooth, coxal hook, and macrosetae of the second tibia. However, these characters should not be used as synapomorphies for genera (Scharff and Coddington, 1997) because they are correlated with body size.

In all geographic data of identified specimens, the names of current political divisions are recorded and measurements are in metric units. Multiple records of very common species are abbreviated to save space.

The following abbreviations are used to identify the source of collections.

ACCH	Academia de Ciencias de Cuba, La Habana, Cuba; L. Armas
AD	A. Dean, Texas A & M University, College Station, Texas, United States
AMNH	American Museum of Natural History, New York, United States; N. Platnick, L. Sorkin
ANSP	Academy of Natural Science, Philadelphia, Pennsylvania, United States; D. Azuma

BMNH Natural History Museum, London, England; P. Hillyard

CAS California Academy of Sciences, San Francisco, California, United States; C. Griswold, W. J. Pulawski, D. Ubick

CBF Coleccion Boliviana de Fauna, La Paz; R. Altamirano

CV Carlos Valderrama A., Bogotá, Colombia

DU D. Ubick, San Francisco, California, United States

FDM F. DelMonte collection, Santo Domingo, Dominican Republic

FSCA Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards

ICNB Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; E. Flórez D.

IMPR Isabella M. P. Rinaldi; Botucatu, Est. São Paulo, Brazil

INPA Instituto Nacional de Pesquisas da Amazônia, Manaus, Est. Amazonas, Brazil

IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; L. Baert

JMM J. Maes, León, Nicaragua

MACN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; E. A. Maury, C. L. Scioscia, M. E. Galiano

MBCV Museo de Biologia, Universidad Central de Venezuela, Caracas, Venezuela; R. Pérez, R. Candia

MCN Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; E. H. Buckup, M. A. L. Marques

MCP Museu de Ciências, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil; A. A. Lise

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States

MECN Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador, Germania Estévez J.

MHNG Muséum d'Histoire Naturelle, Genève, Switzerland; V. Mahnert

MIUP Museo de Invertebrados, Universidad de Panamá, Panama City, Panama; D. Quintero A.

MLP Museo de Universidad Nacional, La Plata, Argentina; R. F. Arrozpide, C. Sutton

MNHN Muséum National d'Histoire Naturelle, Paris, France; C. Rollard

MNHNC Museo Nacional de Historia Natural, La Habana, Cuba; G. Alayón G.

MNRJ Museu Nacional, Rio de Janeiro, Brazil; A. Timotheo da Costa; Adriano Brilhante Kury

MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; D. Silva D.

MZSP Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil; P. Vanzolini, J. L. Leme, R. Pinto da Rocha

MZUF Museo Zoologico de "La Specola" Università di Firenze, Florence, Italy; S. Whitman

NRMS Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Kronestedt

PAN Polska Akademia Nauk, Warszawa, Poland; J. Prószynski, A. Slojewska, W. B. Jedryczkowski, T. Huflejt

REL R. E. Leech, Edmonton, Alberta, Canada

SMF Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; M. Grasshoff

SMNK Staatliches Museum für Naturkunde, Karlsruhe, Germany; H. Höfer

USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., United

States; J. Coddington, S. F. Larcher

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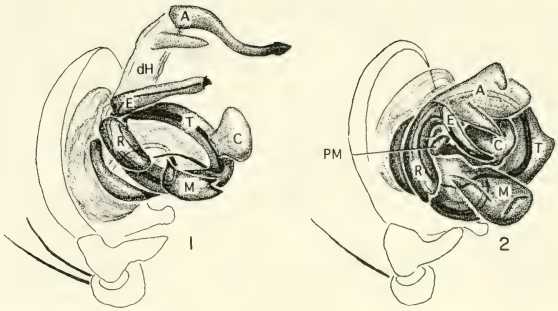
Relationships. Cyclosa, and probably also *Allocyclosa*, may be closest to *Metazygia* and *Eustala*. Synapomorphies with *Metazygia* include the close spacing of the posterior median eyes (Figs. 23, 24), a carapace with few, scattered, fine setae, and having a scape or lobe attached at some length to the base of the epigynum (Levi 1995a, figs. 11, 18; Fig. 33). Close posterior median eye spacing is found in a few other genera such as *Larinia* (Harrod et al., 1991). *Larinia* is close to *Araneus* and not to *Metazygia* because of palpal structures (see below). *Cyclosa vieirae*, a newly described *Cyclosa* with a globular abdomen (Figs. 284–288), although similar to *Metazygia* in appearance, has a *Cyclosa*-like epigynum and palpus (Figs. 290–293).

Cyclosa and *Metazygia* are separated by Scharff and Coddington's (1997) recent cladograms for araneid genera. The cladograms do not provide a convincing phylogeny. [Scharff and Coddington's placement of *Zygiella* as an araneid is correct. See also Piel and Nutt (1997).]

Scharff and Coddington correctly rejected characters that evolved independently in various genera of araneids as well as throughout the Araneae (e.g., stabilimenta of webs). But similar, equally unacceptable characters are used; for instance, the presence or absence of a scape on the epigynum. The scape has evolved independently in *Argiope aurantia* (Levi, 1968), *Zygiella kochi* (Levi, 1974), *Eriophora edax* (Levi, 1970), *Wixia abdominalis*, *Ocrepeira gallianoae* (Levi, 1993) and *Micrepeira hoeferi* (Levi, 1995b). "Scape annulate/or smooth" (Scharff and Coddington, 1997:377, character 31) is another poor character because of homoplasies. *Cyclosa* is listed as having a wrinkled scape, but only *C. conica* has the scape wrinkled (Figs. 42, 44). All other American *Cyclosa* have a smooth scape. Size dimorphism of males and females has evolved numerous times in families of spiders as well as in genera of the Araneidae (e.g., *Argiope*, *Kapogea*, *Manogea* (Levi, 1997), *Allocyclosa*). In *Mecynogea* the males are larger than females; in the related *Kapogea* they are dwarfed. Also size-related are the hook on the first male coxa and a corresponding groove on the second femur, permitting locking of legs when mating. Found in similar-sized partners or when the male is slightly smaller than the female, they are lacking in most species with dwarf males. Unfortunately size ratios and their dependent size-related characters were used by Scharff and Coddington (1997) as characters 1, 2, 32, 33, 34, 45 and 61. They are not synapomorphies for genera.

The stipes is another character used by Scharff and Coddington for phylogeny. But stipes is just the name for the base of the embolus if it is a free sclerite, and it appears in many palpi that have the palpal articles much dissected (e.g., *Argiope*, *Eriophora*). It is a poor phylogenetic character.

On the other hand, an excellent synapomorphy for genera, the paramedian apophysis (PM in Figs. 2, 39), not found in any other family, but found in Araneidae that share other synapomorphies, is alleged by Scharff and Coddington to have



Figures 1, 2. Araneid left palpi, diagrammatic. 1, *Araneus*. 2, *Alpaida*.

Abbreviations. A, terminal apophysis; C, conductor; dH, distal hematodocha; E, embolus; M, median apophysis; PM, paramedian apophysis; R, radix; T, tegulum.

evolved several times. Scharff and Coddington (1997) believe the "conductor lobe", which is apparently homologous to the paramedian apophysis, to have evolved three times. They reject homology of the paramedian apophysis and the conductor lobe because these characters appear in distal lineages in their cladogram (p. 419). But this is the logical result of considering them as separate characters to make the cladogram (p. 373). It is not surprising that an earlier draft of their manuscript had 60,000 possible parsimonious cladograms [as stated by Scharff and Coddington (1997: 403)]. The many homoplasies and later losses of characters used in their present cladogram are disconcerting. The publication states that the palpi were not very useful for the study of phylogeny. One wonders if the examination of several species of each genus would have prevented these errors. (Also see Other Characters below under the genus *Cyclosa*.)

My own views are based on the study of genitalia, including the complex palpi, and the gross morphology of spiders, and are drawn from my generic revisions (Levi, 1995b). The phylogeny used is based on likely apomorphies. The genera of the Araneidae can be naturally arranged into four or five groups: (1) *Argiope* and *Gea*, which have the posterior eye row procurved and have reduced tapetum in the posterior lateral eyes. (2) *Cyrtophora*, *Manogea*, *Mecynogea* and *Kapogea*, which have the aggregate silk glands reduced or lacking and make horizontal dome-shaped webs without viscid silk. Both these groups have been accepted by Scharff and Coddington (1997), and follow Simon (1895). The third and fourth groups are even more distinct, but are confused in Scharff and Coddington. (3) *Araneus* and others that lack a paramedian apophysis in the male palpus have the conductor on the edge of the tegulum, two patellar setae on the palpus and a palpus with a large distal hematodocha (distal hematodocha located between the embolus and terminal apophysis, when expanded, will turn the terminal apophysis) (Fig. 1). They may have the embolus with a cap and a round to oval abdomen, sometimes with shoulder humps or with a posterior median tubercle. (4) The largest clade, with *Alpaida* and *Cyclosa*, includes most of the neotropical araneid genera. They usually have a paramedian apophysis or conductor lobe in the palpus, the conductor in the middle of the tegulum, the embolus without a cap, and only one patellar seta on the palpus (Fig. 2). They lack distal hematodocha but may have macrosetae on the fourth coxae of males, and the abdomen shape is diverse,

frequently with a pair of posterior median tubercles. These paired tubercles are uncommon otherwise in spiders. Not all genera have all of the characters of their clade (e.g., *Eriophora* has two patellar setae on the palpus, some species of *Eriophora* have one and a second weak one; some *Araneus* species have only one). Also, the placement of some genera is uncertain at present.

TAXONOMIC SECTION

Allocyclosa new genus

Type Species. *Cyclosa bifurca* (McCook). The generic name is feminine.

Diagnosis. *Allocyclosa* differs from *Cyclosa* by having the abdomen posteriorly vertically biforked (Figs. 12, 13, 19). Also, the palpus has a different arrangement of sclerites, the conductor is a small tube (C in Fig. 21), the embolus (E) is short but parallel to the conductor and there is a large, complex, soft terminal apophysis (Figs. 20, 22, A in Fig. 21). Unlike the male of *Cyclosa* (Fig. 39) the *Allocyclosa* male lacks a paramedian apophysis in its palpus and has only one patellar seta (Fig. 21). Males are only 35% of female size, there is no tooth on the endite and the hook on the first coxa and the corresponding groove on the second femur are absent.

Relationship. The web in *Allocyclosa* has a vertical stabilimentum, similar to that made by *Cyclosa*.

There are remarkable similarities with *Cyrtophora* species. The biforked tail and humps, not found in other araneids, may be synapomorphies with similar structures in *Cyrtophora* (Levi, 1997, fig. 152). The epigynum with its central area soft (Figs. 6, 11), except for the wide scape in *Allocyclosa*, resembles the anterior edge of the epigynum of *Cyrtophora* (Levi, 1997, fig. 148), and the lateral sclerotization on each side is also similar. Even the palpus has similarities with *Cyrtophora:* the conductor is short, the median apophysis has a spine and the terminal apophysis is soft.

The tapetum of the posterior median eyes is narrow, with rows of rhabdomes on the medial side as in most araneids (not in *Cyclosa*). The posterior lateral eyes may have a narrow tapetum similar to that of *Argiope*.

Natural History. *Allocyclosa bifurca* habits are described in Levi (1977): females sit in the center of the web, as does *Cyclosa*. Above the spider is a line of overlapping egg sacs; below the spider is a line of detritus or wrapped prey. The spider is difficult to find. *Allocyclosa bifurca* appear to be social, and males are very uncommon.

Distribution. Only one species is known, distributed from Florida to western Panama.

Allocyclosa bifurca (McCook), new combination
Figures 3–22; Map 1

Cyrtophora bifurca McCook, 1887: 342. Female, male syntypes from Fairyland, Merrit's Island, on the Indian River, Florida, in ANSP, lost.

Cyclosa fissicauda O. P.-Cambridge, 1889: 49, pl. 8, fig. 7, ♀. Fifteen syntypes in two vials from near Dolores, Guatemala, in BMNH, examined. Keyserling, 1893: 274, pl. 14, fig. 203, ♀.

Cyclosa bifurca:—McCook, 1894: 227, pl. 17, figs, 9, 10, ♀, ♂. F. P.-Cambridge, 1904: 495, pl. 47, fig. 8, ♀, ♂. Roewer, 1942: 759. Bonnet, 1956: 1309. Levi, 1977: 86, pl. 5, figs. 78–89, ♀, ♂, map 2.

Cyclosa furcata O. P.-Cambridge, 1889: 247, pl. 31, fig. 3, ♀. Female syntypes from Amula, Guerrero, Mexico, in BMNH, examined. F. P.-Cambridge, 1904: 494, pl. 47, fig. 6, ♀, examined. Roewer, 1942: 760. Bonnet, 1956: 1316. NEW SYNONYMY.

Note. F. P.-Cambridge separates *C. furcata* from *C. bifurca* on the basis of the lack of dorsal, abdominal tubercles in *C. furcata*. But these are present in the syntype of *C. furcata* that I illustrated in 1975 (in my notes). Perhaps shrivelling with age emphasized previously inconspicuous tubercles. The specimen of *C. furcata* examined has a triangular-shaped scape (Figs. 9–11), which I believe is within the variation of *C. bifurca*.

Description. Female from Nuevo Léon, Mexico. Carapace yellowish (Fig. 13).

Map 1. Distribution of *Allocyclosa bifurca*.

Sternum dark brown with median and paired lateral white patches. Legs yellowish with narrow dark rings. Abdomen white with some indistinct, dorsal, paired dusky patches; venter with a pair of white bands, spinnerets brown with a narrow surrounding black ring (Figs. 13, 14). Posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.7 diameter, posterior laterals one diameter. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.3 diameter apart, 2.1 diameters from laterals. Ocular trapezoid longer than wide, narrower behind than in front. Height of clypeus equals 0.9 diameter of anterior median eye. Abdomen with two pairs of humps and a biforked, median, posterior extension (Fig. 12). Total length 7.8 mm. Carapace 2.9 mm long, 2.2 wide in thoracic region, 1.1 wide behind posterior lateral eyes. First femur 3.4 mm, patella and tibia 3.5, metatarsus 2.1, tarsus 1.0. Second patella and tibia 3.1 mm, third 1.8, fourth 2.7. First and third femora the same length as corresponding patella and tibia, second and fourth slightly shorter.

Male from Florida. Cephalothorax yellowish white with large black eye rings. Legs with narrow black rings at distal ends of some articles. Abdomen white pigmented except in cardiac area, genital area and spinnerets, all of which are yellowish white. Posteriorly, dorsum has several indistinct black transverse lines of tiny black pigment spots (Fig. 19). Posterior median eyes 0.6 diameter of anterior medians, anterior laterals 0.3 diameter, posterior 0.6 diameter. Anterior median eyes 1.2 diameters apart, 0.4 diameter from anterior laterals. Posterior median eyes separated by 0.7 diameter, 2 diameters from posterior laterals. Ocular quadrangle is a trapezoid, as in female, wider than long, widest in front. Clypeus length equals 1 diameter of anterior median eye. Endite without tooth. Palpal patella with one macroseta. First coxa without hook. Abdomen with lateral and posterior tubercles indistinct. Total length 1.8 mm. Carapace 0.85 mm long, 0.77 wide in thoracic region, 0.39 wide behind posterior lateral eyes. First femur 1.10 mm, patella and tibia 1.10, metatarsus 0.62, tarsus 0.42. Second patella and tibia 0.87 mm, third 0.43, fourth 0.66. All femora slightly longer than corresponding patella and tibia.

Note. Living specimens are transparent green, with a red patch on the underside between epigynum and spinnerets. Both red and green pigments wash out in the preserving fluid.

Males are uncommon; they have paired tubercles at the posterior of the abdomen, as in the female.

Variation. Total length of females 5.1 to 8.5 mm. Figures 6 to 8 and 12 were made from a female from Nuevo Léon, Mexico,

Figures 9 to 11, 13, 14 were made from a syntype of *C. furcata*. Figures 3 to 5 and the male illustrated came from Dade County, Florida.

Diagnosis. Both body shape (Figs. 12–14) and lightly sclerotized genitalia separate this species from *Cyclosa*.

Natural History. Collected in the United States under eaves of buildings and in date palm, in Mexico by sweeping palmetto thicket in San Luis Potosí, in short tropical rain forest in Campeche, in thorn forest in Baja California Sur and on agave and *Pina raron* in Cuba.

Distribution. Florida, Texas and Baja California south to western Panama, Cuba and Hispaniola (Map 1).

Specimens Examined. UNITED STATES *Florida*: *Citrus Co.*: 1♀ (Weed, MCZ). *Dade Co*: Crandon Park, 27 Nov. 1952, 1♂ (A. M. Nadler, AMNH); Coral Gables, 11 Mar. 1976, 2♀ (V. Brach, MCZ). *Hillsborough Co.*: Hillsborough River State Park, 1♀ (MCZ). *Indian River Co.*: Sebastian, Dec. 1921, 3♀; Jan. 1922, 3♀; 30 Nov. 1931, 2♀; Jan, Feb 1945, 1♀ (G. Nelson, MCZ). *Palm Beach Co.*: Palm Beach, Mar. 1909, 1♀ (F. Winslow, MCZ); Apr. 1920, 1♀ (T. Barbour, MCZ); Lake Worth, Apr. 1891, 2♀ (G. W. Peckham Coll., MCZ). *St. Johns Co.*: 27 Mar. 1959, 2♀ (J. McCrone, MCZ). *Alabama*: *Baldwin Co.*: Silverhill, Apr. 1946 1♀ (G. Nelson). *Texas*: *Aransas Co.*: Goose Isl. State Park, 15 June 1961, 4♀ (A. R. Brady). *Hidalgo Co.*: Pharr, 26 Dec. 1941, 1♀. *Kenedy Co.*: 1.6 km S Riviera, 14 Nov. 1958, 1♀ (A. R. Brady); 46 km S Sarita, 14 Nov. 1958, 1♀ (A. R. Brady). *San Patricio Co.*: Lake Corpus Christi Dam, 28, 29 May 1983, 1♀ (W. Maddison). MEXICO *Nuevo Léon*: Cola de Caballo, 21 May 1973, 3♀ (MCZ). *Baja California Norte*: Ceralba [Cerralvo] Isl., 7 June 1921, 2♀ (J. C. Chamberlin, MCZ). *Baja California Sur*: La Paz, 5 June 1921, 2♀ (J. C. Chamberlin, CAS, MCZ); E of La Paz, 7 Sept. 1963, 1♀ (P. R. Craig, W. Hill, CAS); 9.6 km W San José del Cabo, Jan 1982, 6♀ (D. Ubick, DU); Chalba Isl., 7 June 1921, imm. (J. C. Chamberlin, CAS). *San Luis Potosí*: Valles El Bañito, 27 June 1940, 1♀ (H. Hoogstraal, MCZ); Valles, hotel, 1961, 1♀ (L. Steude, AMNH). *Veracruz*: 12 km NW Alvarado, Highway 180, 18°50′N, 95°51′W, 28 June 1983, 1♀ (W. Maddison, R. S. Anderson, MCZ); Lago Catemago, La Jungla, 18°27′N, 95°05′W, 19 July 1991, 5♀ (W. H. Piel, G. S. Bodner, MCZ); Las Tuxtlas, 15 km N Catemaco, 50 m, Aug. 1986, 3♀ (W. Eberhard FNS-31, MCZ). *Hidalgo*: 4.8 km N Chapulhuacan, 21°11′N, 98°54′W, 20 April 1963, 1 imm. (W. J. Gertsch, W. Ivie, AMNH). *Distrito Federal*: México, Fall 1940, 1♀ (H. Wagner, AMNH). *Campeche*: Chicama Ruins, 8 km W Xpujil, 18°32′N, 89°31′W, 12–14 July 1983, 1♀ (W. Maddison, MCZ). GUATEMALA *Petén*: Tikal, 7 July 1975, 2♀ (W. Sedgwick, MCZ); Petén Poptun, Finca Ixobel, 7 Feb. 1980, 1♀, (V. Roth, AMNH). HONDURAS *Atlántida*: Lancetilla, July 1929, 2♀, 4 imm. (A. M. Chickering, MCZ). COSTA RICA *Heredia*: 15 km S Pto. Viejo, El Plastico, Feb. 1989, 1♀ (W. Eberhard, MCZ). *San José*: San José, 30 Sept. 1980, 1♀ (W. G. Eberhard, R. W. Work, MCZ). PANAMA *Chiriquí*: Bugaba, 2 Nov. 1985, 1♀ (D. Quintero, MIUP).

CUBA *Holguin*: Banes, Aug. 1955, 6♀ (A. F. Archer, AMNH). HISPANIOLA *Dominican Republic*: Puerto Plata, Apr., May 1941, 3♀ (D. Hurst, MCZ).

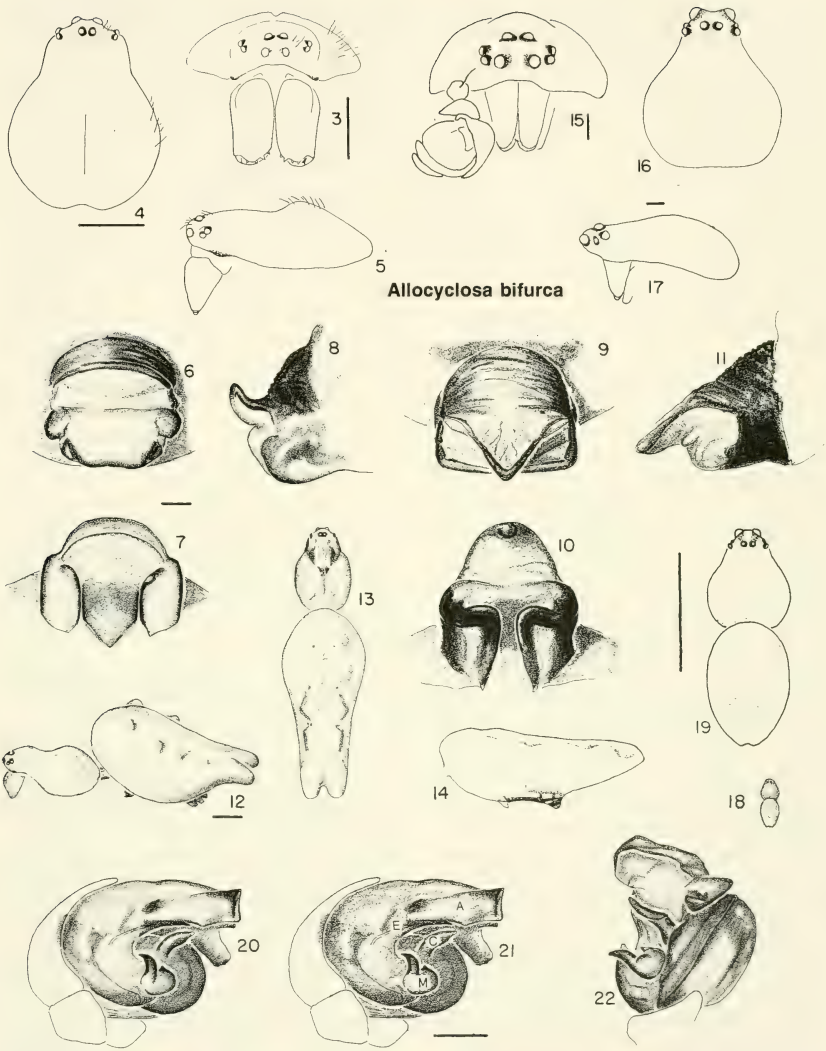
Cyclosa Menge

Cyclosa Menge, 1866: 73. Type species *C. conica* (Pallas) by monotypy. Neave, 1939: 922. The gender of the name is feminine (Bonnet, 1956: 1306).

Turckheimia O. P.-Cambridge, 1889: 46. Type species *T. nodosa*, designated by F. P.-Cambridge, 1904: 491. First synonymized with *Cyclosa* by F. P.-Cambridge (1904: 491).

Parazygia di Caporiacco, 1955: 345. Type species *P. accentonotata* di Caporiacco [=*C. tapetifaciens* Hingston). First synonymized by Levi (1977: 73).

Diagnosis. *Cyclosa* belongs to a group separated from other araneid genera by having a paramedian apophysis in the palpus, posterior median eyes adjacent and, unlike most araneid genera (except *Zygiella*), a full canoe-shaped tapetum in the posterior median eyes [i.e., lacking the araneid modification of a narrow tapetum with rows of rhabdomes toward the median of the spider (Homann, 1950)]. Unlike many araneids, *Cyclosa* usually has an abdomen that is longer than wide and that extends posteriorly beyond the spinnerets (Figs. 46, 66). There are black, paired, irregular marks or lines on the abdomen (Figs. 46, 59, 64) and between the genital groove and spinnerets; the venter has a pair of white patches separated by some distance from one another (Figs. 60, 90, 100). The pair of white patches may be on tubercles and may be separated by a third, median white patch (Figs. 100, 202). There is a black ring around the spinnerets. The cephalic region of males is less than half the width of the thorax (Fig. 28), and the length of the horizontal clypeus is equal to about 2 diameters of the anterior



Figures 3–22. *Allocyclosa bifurca* (McCook). 3–14, female. 3, eye region and chelicerae. 4, carapace. 5, carapace and chelicera, lateral. 6–11, epigynum. 6, 8, ventral. 7, 10, posterior. 8, 11, lateral. 12, sublateral. 13, dorsal. 14, abdomen lateral. 15–22, male. 15, eye region, chelicerae and right palpus. 16, carapace. 17, carapace and chelicera, lateral. 18, male in same proportion as Figures 12 and 13. 19, male dorsal. 20–22, left palpus. 20, 21, mesal. 22, ventral.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; M, median apophysis.

Scale lines: 1.0 mm; Figures 15–17 and palpi 0.1 mm.

median eye (Fig. 29). In many species there are additional tubercles on the abdomen (Figs. 277, 328, 348).

Most distinct are the genitalia: an epigynum divided by a scape (Fig. 31), sometimes annulate (*C. conica*, Figs. 42, 44), weakly sclerotized with an anterior depression on each side of the base of the scape, and an indistinct, almost invisible opening on each side (Fig. 31). The bulb of the palpus is usually wider than long, with a huge conductor holding the embolus in a gutter (Figs. 39, 41) and the base of the median apophysis close to the conductor.

All *Cyclosa* have long femora, the third often equal to or longer than the combined patella and tibia. (Sometimes the specimen used to measure these proportions is different from the one described.)

Description. Female. Carapace with few setae (Fig. 24). Sternum usually marked with a light anterior transverse bar and five light patches, both with indistinct borders (Fig. 38). Legs of most species yellowish with dark rings. Eyes subequal (Figs. 23, 24). Median eyes form a trapezoid, wider in front, usually slightly longer than width at anterior eyes (Figs. 23, 24). Anterior median eyes of females their diameter apart or slightly less, about the same distance or slightly more from laterals. Posterior median eyes touching to 0.4 diameter apart, 1.2 to 4 diameters from laterals (Figs. 23, 24). The height of the clypeus is slightly less than the diameter of the anterior median eyes. All species have similar genitalia, but the abdomen shape is variable. Abdomen often with pairs of tubercles (Figs. 277, 357, 372). Rarely, tubercles and posterior overhang are lost, as in *C. olivenca* and *C. vieirae* (Figs. 288, 296); nevertheless, genitalia place both with *Cyclosa*. In other parts of the world some *Cyclosa* species have a silvery abdomen.

Male. Males with anterior eyes separated by about their diameter, or slightly less, and about the same distance from laterals. Posterior median eyes touching or to about 0.3 diameter apart and 1.5 to 3 diameters from laterals. Clypeus horizontal, almost parallel with sternum, and its length is 2 to 3 diameters of anterior median eye. All males with one strong patellar macroseta (Fig. 27). Males between 80 and 110% of size of female (as measured by width of carapace). All with a tooth on the endite facing the femur (Fig. 27), a minute hook on first coxa, laterally on posterior margin, and with a minute corresponding groove on second femur. Of species examined, only male of *C. conica* had a pair of macrosetae on fourth coxae (Fig. 48). Second tibiae (Fig. 30) usually with stronger setae than first.

Other Characters. Scharff and Coddington (1997) attribute additional characters to *Cyclosa: Cyclosa* is stated to have grooves and wrinkles on the booklung covers (p. 366). All araneids and tetragnathids (but apparently not theridiids) have corrugations on booklung covers if the size of the spider is larger than 8 to 10 mm. Presumably the corrugations strengthen the plate. American *Cyclosa* are small and lack these grooves and wrinkles, but they are present in *C. diversa* (12 mm) and *C. nodosa* (9.5 mm).

Scharff and Coddington's clade no. 50 indicates the paramedian apophysis is lost. On the contrary, it is usually present (Fig. 39). In the large *C. bifurcata*, if the conductor is torn off, the paramedian apophysis stays attached to the tegulum. In *C. caroli* and *C. tapetifaciens*, the paramedian apophysis is attached to the membrane that connects conductor and tegulum. Only in *C. conica* does the paramedian apophysis attach to the conductor and appear as a lobe.

Clade no. 53 indicates the palpal conductor has a lobe. Usually no lobe is present, except in *C. conica*.

Clade no. 42 indicates that the carapace of *Cyclosa* is hairy. Not so. I have found only scattered fine setae on the *Cyclosa* specimens I examined.

Clade no. 43 indicates the palpus has a distal hematodocha and a terminal apophysis. American *Cyclosa* however lack a dis-

Map 2. Approximate number of *Cyclosa* species known from American regions.

tal hematodocha and often only have rudiments of the terminal apophysis (A in Fig. 39). A membrane between sclerites permits movement, but an expandable hematodocha is present only between the cymbium and subtegulum.

Genitalia. The conductor of the male palpus of *Cyclosa tapetifaciens* was examined carefully. In the left palpus it is attached with a small amount of soft tissue, in a small area to the left of the center of the tegulum. The soft tissue permits movement of the structure. The stalk of the paramedian apophysis (Fig. 39) is attached to the same, soft tissue; it is not attached to the conductor (except in *C. conica*).

Function of the genitalia. During mating, the tooth of the conductor hooks into the depression of the female's epigynum. Occasionally (but often in *C. diversa*) the tooth may break off (Figs. 411, 412) and remain stuck in the depression (Figs. 395, 396, 399). When this happens only one tooth is found per side.

The long filiform embolus enters an opening in the epigynum (Figs. 31, 32) that is not sclerotized and is difficult to see. (My observation in 1977 on the course of the embolus in the duct was wrong.) After entry, the embolus makes a distinct loop, visible in some epigyna through the lightly sclerotized median plate (Figs. 32,

87), and follows a canal along the margin of the posterior lateral plates around the median plate before entering the seminal receptacles (Figs. 32, 34–37). In a single female of four different species, the embolus had broken during mating and remained in the epigynum.

Relationship. The posterior median eyes of all *Cyclosa* have a canoe-shaped tapetum, a primitive character otherwise found only in *Zygiella* among the Araneidae (Homann, 1950).

All neotropical *Cyclosa* species have genitalia similar to the genitalia of nearctic *C. caroli* (Figs. 162–166, 173) and *C. turbinata* (Figs. 314, 315, 318). In all other *Cyclosa*, including *C. conica* (Figs. 42–45, 47), a holarctic species that extends into northern Mexico, the genitalia have heavier sclerotization, including the lobes and plates of the epigynum (Figs. 42, 43), and also have the palpal sclerites and the epigyna more diverse (Levi, 1977, figs. 21–37; Fig. 47). Also, *C. conica* is the only species in the Americas having a terminal apophysis (in the shape of an upside-down swimming duck, at 10h in Fig. 47). In the other American species, the conductor (C in Fig. 39) and median apophysis (M in Fig. 39) are similar in shape from species to species, and the terminal apophysis is lost or has a transparent, filiform line (A in Figs. 39, 40).

The differences among American *Cyclosa* species are limited to the relative proportions of the structures in the female epigynum and to minor differences in the tooth of the conductor and the armature of the median apophysis in the male palpus.

The details of the palpal structures of American *Cyclosa* males indicate interspecies relationships better than characteristics of the epigyna. In particular, males with a barb (Fig. 39) on the median apophysis, and a conductor tooth shaped like a parrot's beak (Fig. 41) probably are closely related. These criteria result in grouping females that may have the abdomen differently shaped (e.g., *C. walckenaeri* and *C. turbinata*). I was not able to match males with females by comparing the structure of the epigynum with that of the palpus.

Natural History. All species make a fine-meshed vertical web with a vertical stabilimentum, the upper half of which may consist of overlapping egg sacs. The spider rests in the center and is difficult to see (Levi, 1977, pls. 1–4). The lower half of the stabilimentum consists of detritus and stored, wrapped food. The webs of *C. diversa* and *C. nodosa* have golden threads; others are known that have white silk (W. G. Eberhard, personal communication).

Distribution. *Cyclosa* species are found world-wide.

Misplaced Species.

Cyclosa brevis:—Alayón, 1993: 2, fig. 1, is an unnamed female *Wagneriana*.

C. convexisterna di Caporiacco, 1947: 25, is an immature *Mecynometa* (Tetragnathidae). NEW COMBINATION.

C. minuscula Mello-Leitão, 1940a: 179, is a *Dolichognatha* (Tetragnathidae). NEW COMBINATION.

C. olivierioi Soares and Camargo, 1948: 655, fig. 62, ♂, is an *Alpaida* male (with both palpi lost). NEW COMBINATION.

C. paranensis Mello-Leitão, 1937: 7, fig. 7, ♀, is a *Mecynometa* (Tetragnathidae). NEW COMBINATION.

C. punctata Keyserling, 1880: 312, pl. 4, fig. 14, ♀, from Rio de Janeiro State, Brazil, is of uncertain placement. (See Appendix and Figs. 433, 434.)

C. v-notata Petrunkevitch, 1925: 115, fig. 29–31, ♀, is *Argyrodes caudatus* (Taczanowski), Theridiidae. NEW SYNONYMY.

Larinia silvestris Bryant, 1942: 5, figs 5, 7, 10, 11, ♀, ♂, erroneously placed in *Cyclosa* by Harrod at al. (1991), is a *Metazygia*. NEW COMBINATION. (See Appendix and Figs. 430–432.)

Turckheimia moraballi Hingston, 1932: 369 is *Parawixia kochi* (Taczanowski) (Levi, 1995a).

T. tuberculata Hingston, 1932: 368 is *Parawixia kochi* (Taczanowski) (Levi, 1995a).

Unknown Species.

Cyclosa tricolor Mello-Leitão, 1940b: 202, changed by Brignoli (1983: 266) to *C. tricolorata*, has type lost.

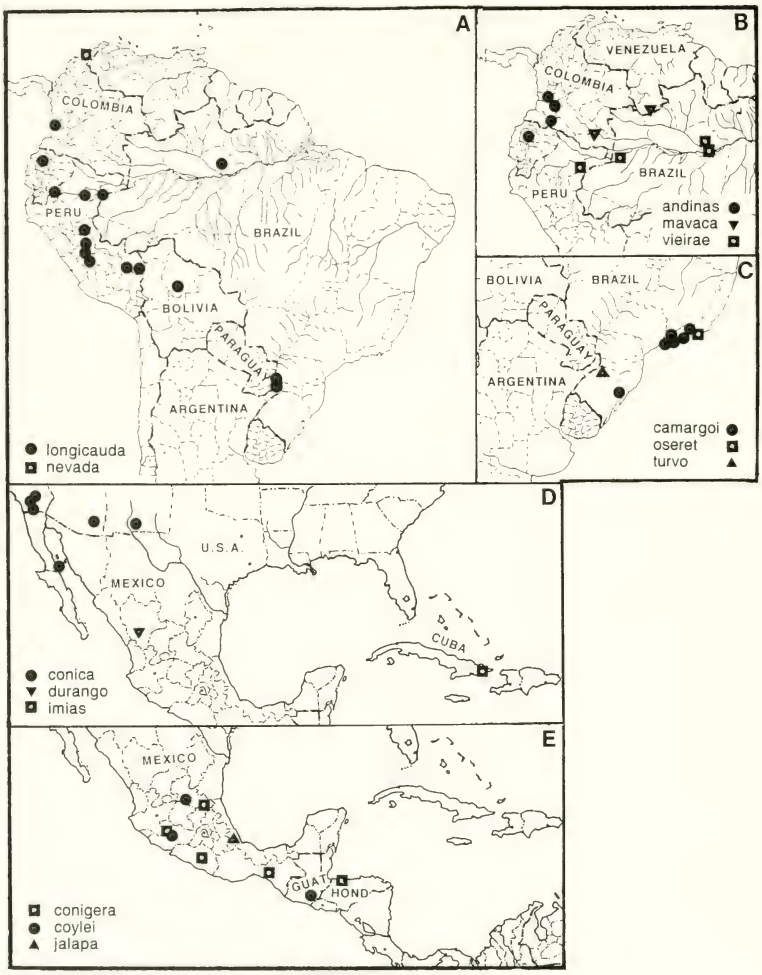
Separating American Species. Specimens from different localities often differ in details of their genitalia, as do individ-

uals of the same species collected in the same area. Although the relatively soft epigyna are all quite similar, females can be separated by the shape of the abdomen. Nevertheless, females that have oviposited or dried up may have tubercles that are not found in a well-fed and well-preserved individual (Fig. 170).

Separating males presents a challenge. In some species the abdomen of a large male is similar to that of the female, but in smaller individuals differs by lacking tubercles and may have an oval shape. For males, the abdomen should be used as a last resort to distinguish between species with similar palpi. Diagnostic features of males include the sclerotized tooth of the conductor (Fig. 41), which is almost always partly hidden by a flap attached to the tip of the gutter (Fig. 41), the armature of the median apophysis (at 4h in Fig. 39), which may be partly hidden by the overhanging conductor and the tip of the conductor in apical view (Fig. 83). But the tip of the conductor in apical view is more variable than the armature of the median apophysis. The embolus, a thread in the gutter of the conductor, with its swollen base visible on the dorsal side of the palpus (at 3h in Fig. 375), is similar in all species. Above the embolus (Fig. 375) lies the soft terminal apophysis, an indistinct structure in all American species.

Key to Female Mexican and Neotropical *Cyclosa*

1. Abdomen with 5 or 6 tubercles (Figs. 328, 357, 372, 420) 2
– Abdomen with fewer tubercles (Figs. 46, 80, 269, 277, 296) 15
2(1). Abdomen with 5 tubercles, or 6 with median, posterior, upper tubercle minute (Figs. 365, 367, 370–372) 3
– Abdomen with 6 tubercles (Figs. 382, 389, 390, 402, 403, 420) 5
3(2). Epigynum scape with narrow neck (Fig. 368); widespread (Map 8A) ..... *bifurcata*
– Epigynum with wide scape without neck, as in Figures 354, 363 4
4(3). Hispaniola, Jamaica, Puerto Rico (Figs. 363–367; Map 8A) ..... *haiti*
– Argentina, Chile (Figs. 354–358; Map 6E) ..... *serena*
5(2). Anterior pair of tubercles bulbous (Figs. 415, 420, 423, 427) 6
– Anterior pair of tubercles small (Figs. 389, 404) 9
6(5). Abdomen with lightly sclerotized plates (Figs. 423, 427) 7
– Abdomen with streaks 8
7(6). Central America (Map 6F); epigynum as in Figures 425, 426 ..... *nodosa*
– Cuba (Map 6F); epigynum as in Figures 421, 422 ..... *alayoni*
8(6). Trinidad (Map 6F); epigynum as in Figures 417, 418 ..... *tamanaco*
– Curaçao (Map 6F); epigynum as in Figures 413, 414 ..... *ojeda*
9(5). Scape club-shaped, narrow, long, widest at distal end (Figs. 387, 391, 393, 395, 397) 10
– Scape otherwise (Figs. 322, 324, 333, 335, 344, 354, 363) 11
10(9). A diagonal groove on each side of epigynum in posterior view (at 10h, 2h in Fig. 388); Mato Grosso, southern Brazil to northern Argentina (Map 6E) ..... *vicente*
– No such groove (Figs. 392, 394, 396, 398, 400); widespread (Map 8B) ..... *diversa*
11(9). Scape circular and stalked (Fig. 378); Costa Rica (Map 8B) ..... *jose*
– Scape with more or less parallel sides (Figs. 322, 333, 344) 12
12(11). Abdomen short, almost as wide as long (Figs. 346, 348); Baja California (Map 7A) ..... *pichilinque*
– Abdomen longer than wide (Figs. 337, 338) 13
13(12). Scape narrow, 3 to 5 times as long as wide, with parallel sides (Figs. 333, 335); Florida, southern Texas to West Indies, Guianas (Map 7A) ..... *walckenaeri*
– Scape wider, 1.3 to 2.5 times as long as wide (Figs. 322, 324, 354); posterior median plate small (Figs. 323, 325, 355) 14
14(13). Scape wide, 1.5 times as long as wide (Figs. 322, 324); posterior median plate small (Figs. 323, 325); California to Peru (Map 7B) ..... *berlandi*
– Scape narrow, 2.5 times as long as wide (Fig. 354); posterior median plate lobed (Fig. 355); Argentina, Chile (Map 6E) ..... *serena*
15(1). Abdomen spherical, with or without posterior median tubercle (Figs. 288, 296); Amazon area 16
– Abdomen elongate with a median, dorsal posterior extension (Figs. 251, 277, 308, 316) 17
16(15). Abdomen with posterior dorsal knob (Figs. 296, 297); Amazon area (Map 6D) ..... *olivenca*
– Abdomen without posterior dorsal knob



Map 3. Distribution of *Cyclosa* species.

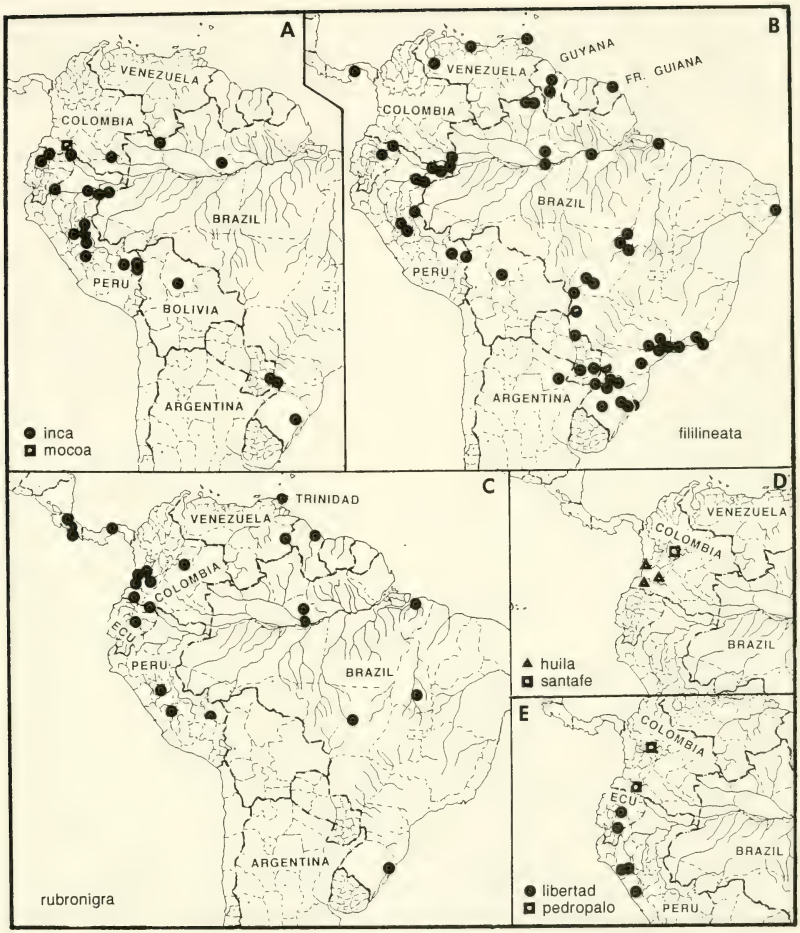
(Figs. 288, 289); Amazon area (Map 3B) ..... *vieirae*

17(15). Abdomen with an anterior pair of dorsal tubercles (Figs. 235, 277, 316) 18

– Abdomen without anterior pair of tubercles (Figs. 46, 56, 61) 25

18(17). Anterior pair of tubercles tipped by nipples (Fig. 277); Mexico, Lesser Antilles to Venezuela and Peru (Map 6D) ..... *triquetra*

– Anterior pair of tubercles rounded (Figs. 235, 259, 308) 19



Map 4. Distribution of *Cyclosa* species.

19(18). Scape of epigynum narrow, its length more than 4 times its width (Figs. 49, 50); Cuba (Map 3D) ..... *imias*

– Scape wider, length about 2 to 3 times its width (Figs. 304, 314) 20

20(19). Cuba, Mexico, Central America, Galapagos 21

– South America 22

21(20). Epigynum with large circular openings (Figs. 304, 305); Costa Rica to Panama (Map 6B) ..... *monteverde*

– Epigynum with small openings near posterior margin (Figs. 314, 315); United States, to Panama, Bermuda, Greater Antilles, Galapagos (Map 6A) ..... *turbinata*

22(20). Peru 23

– Southeastern South America 24

23(22). Openings anterior in ventral view and at

an angle to the median (Fig. 236); Ecuador, western Peru (Map 4E) ..... *libertad*

– Openings in midline of epigynum and almost parallel (Fig. 232); Peruvian Andes (Map 5C) ..... *cajamarca*

24(22). Openings seemingly in a loop on each side of scape (Fig. 265); southern Brazil (Map 6C) ..... *machadinho*

Openings on sides (Fig. 256); on each side of scape a granulated surface or dried mucus (Fig. 256); southern Brazil (Map 6G) ..... *morretes*

25(17). Scape circular with a neck (Figs. 162, 165, 199, 204, 208, 212) 26

– Scape elongate (Figs. 42, 195) 30

26(25). Scape width greater than width of base on each side (Figs. 208, 209); Amazon area (Map 3B) ..... *navaca*

Side of epigynum base wider on each side than width of scape (Figs. 199, 204, 212) 27

27(26). Width of base on each side of scape about 1.5 times width of scape (Figs. 212, 214); body cylindrical (Figs. 216, 217); southern Brazil (Map 3C) ..... *camargoi*

– Width of base on each side is 1.5 times or more than scape width, abdomen narrows posteriorly, cone-shaped (Figs. 203, 206) 28

28(27). Brow almost vertical on each side of scape (Fig. 204); southern Brazil (Map 3C) ..... *turvo*

– Epigynum otherwise 29

29(28). A distinct, circular depression on each side of scape neck (Fig. 199); southeastern Brazil (Map 3C) ..... *oseret*

– Depression hidden under each side of neck of scape, often with circular brows (Figs. 162, 164, 165); widespread (Map 5D) ..... *caroli*

30(25). Scape wide, pointed, with brow posterior to base of scape (Fig. 195, 196); northern Bolivia (Map 5B) ..... *donking*

– Epigynum otherwise 31

31(30). Abdomen short and wide (Fig. 46); in lateral view, spinnerets near midline or in posterior half of abdomen (Figs. 46, 76, 91, 149, 157, 187, 227) 32

Abdomen elongate, spinnerets in anterior half of abdomen (Figs. 61, 66, 70, 112, 121) 40

32(31). Scape with annuli (Fig. 42); base of epigynum with sclerotized, lateral lobes folded over median area (Fig. 42); holarctic to northern Mexico (Map 3D) ..... *conica*

– Scape without annuli (Fig. 31); base of epigynum otherwise (Fig. 31) 33

33(32). Depression and brow on each side of scape wider than side of base of epigynum (Fig. 223); Peruvian Amazon area (Map 5C) ..... *dianasilvae*

– Epigynum otherwise 34

34(33). Epigynum with sclerotized triangle on each side, lateral to base of scape (Figs. 71–73); Mexico (Map 3D) ..... *durango*

– Epigynum without these triangles (Figs. 86, 146) 35

35(34). Epigynum with lip of opening circular (Figs. 86, 146) 36

– Epigynum with straight openings (Figs. 181, 183, 154, 240, 248) 37

36(35). Posterior lateral plates narrow, median area large (Fig. 87); widespread (Map 4A) ..... *inca*

– Posterior median area small (Fig. 147); Bogota, Colombia (Map 4D) ..... *santafe*

37(35). Scape wide, about as wide as cross-section of brow on each side (Figs. 181, 183); widespread from Panama to northern Argentina (Map 5A) ..... *tapetifaciens*

– Epigynum otherwise 38

38(37). Depression on each side with two lips (Fig. 154); southern Colombia (Map 4D) ..... *huila*

– Depression with one lip in ventral view (Fig. 248) 39

39(38). Epigynum as in Figure 248; Pantanal area, Mato Grosso (Map 6G) ..... *pantanal*

– Epigynum as in Figure 240, with scape narrow; Bolivia (Map 5C) ..... *curiraba*

40(31). A wide groove below scape, appearing as a wide notch on anterior margin in posterior view (Fig. 119); Amazon, western Peru to northern Argentina (Map 3A) ..... *longicauda*

– Epigynum without groove under scape (Figs. 58, 63, 87, 97) 41

41(40). Depression and brow on each side of scape wider than area lateral to it (Fig. 57); Mexico to Honduras (Map 3E) ..... *conigera*

– Epigynum base with lateral area wider than depression (Fig. 96) 42

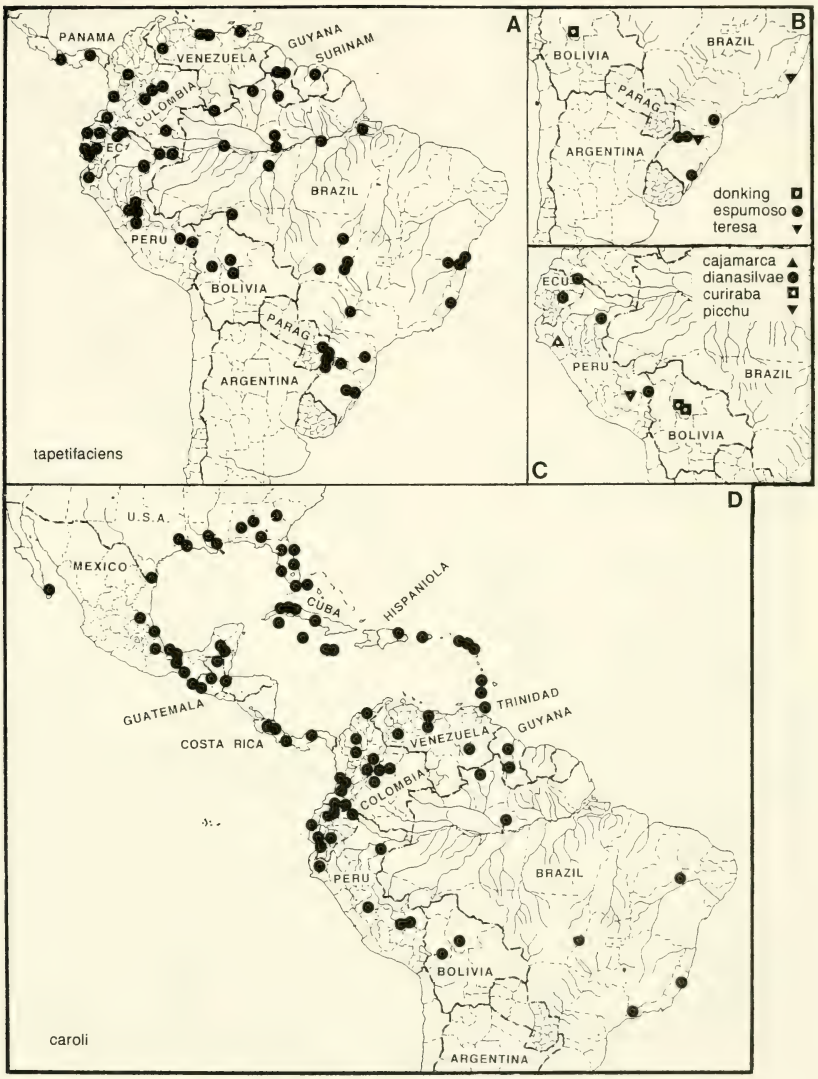
42(41). Depression diameter less than width of scape (Figs. 96, 98), depression circled by brow; Mexico to northern Argentina (Map 4B) 43

– Depression diameter wider than width of scape (Figs. 62, 77, 86) 44

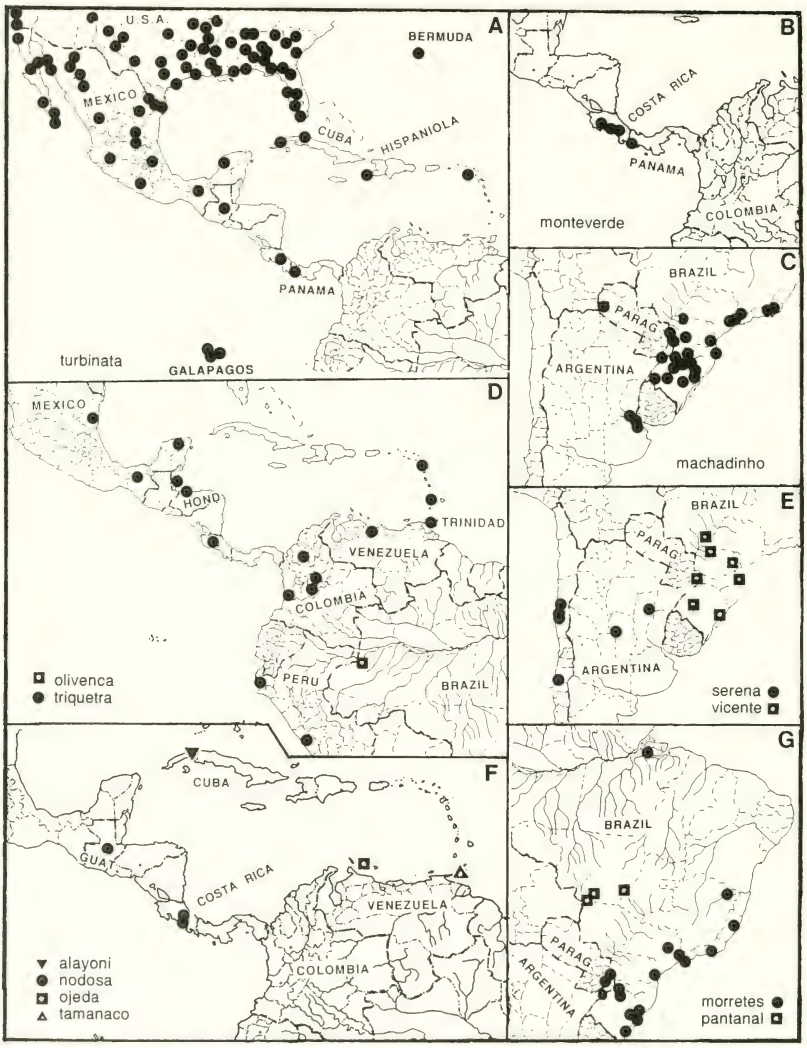
43(42). Abdomen cylindrical, with posterior swelling (Figs. 216, 217); southern Brazil (Map 3C) ..... *camargoi*

– Abdomen tapering to a point posteriorly (Figs. 99–101); Mexico to northern Argentina (Map 4B) ..... *fililineata*

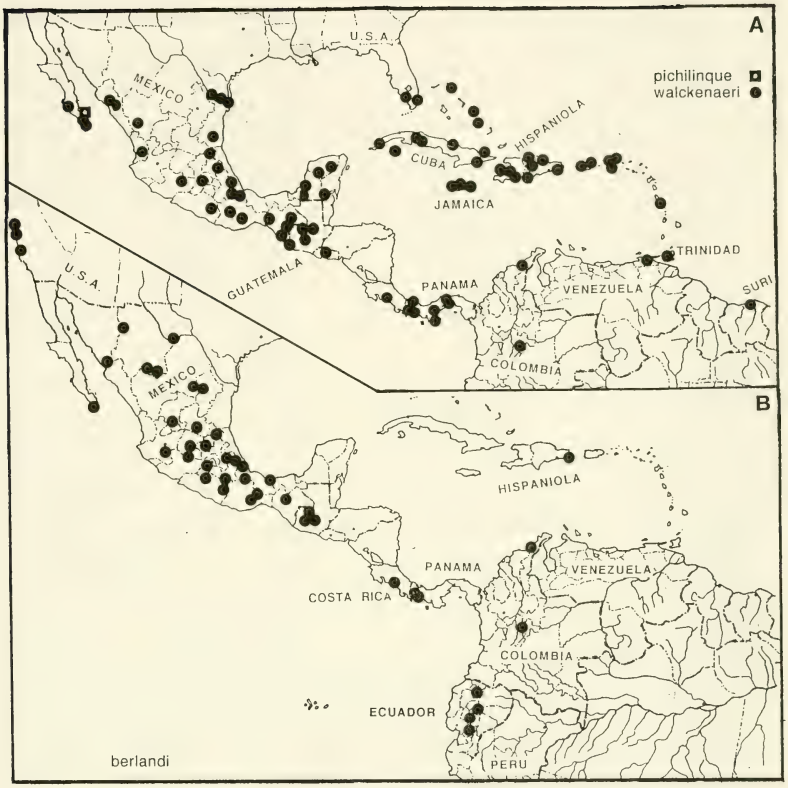
44(42). Opening with large circular lip, about its diameter from scape (Figs. 77, 86, 108) 45



Map 5. Distribution of *Cyclosa* species.



Map 6. Distribution of *Cyclosa* species.



Map 7. Distribution of *Cyclosa* species.

– Opening with straight lip or slightly curved lip (Figs. 53, 62, 67, 138) 47

45(44). Depression of epigynum with a brow (Figs. 78, 87) 46

– Depression of epigynum without brow (Fig. 108); southern Colombia to northern Ecuadoran Andes (Map 3B) ..... *andinas*

46(45). In posterior view, lateral plates narrow (Fig. 87); widespread (Map 4A) ..... *inca*

– In posterior view, lateral plates wider (Fig. 78); widespread (Map 4C) ..... *rubronigra*

47(44). Mexico 48

– Colombia to Peru 49

48(47). A deep, wide depression on each side of base of scape (Fig. 62); Mexico, Guatemala (Map 3E) ..... *coylei*

– Anterior lip and brow of depression on each side of base of scape (Fig. 53); Mexico (Map 3E) ..... *jalapa*

49(47). Ecuador, Peru; epigynum with straight openings at an angle to median axis (Fig. 236) ..... *libertad*

– Colombia; epigynum otherwise (Figs. 67, 127, 138) 50

50(49). Opening posterior, not visible in ventral view (Fig. 128); northern Colombia mountains (Map 3A) ..... *nevada*

– Opening visible ventrally 51

51(50). Posterior median plate wider than long

(Fig. 139); Depto. Cundinamarca, Colombia (Map 4E) ..... *pedropalo*

– Posterior median plate as wide as long (Fig. 68); southern Colombian Andes (Map 4A) ..... *mocoa*

KEY TO MALE MEXICAN AND NEOTROPICAL *CYCLOSA*

1. Fourth coxa with two macrosetae (Fig. 48); a large, nonsclerotized terminal apophysis with wrinkles (at 10h in Fig. 47); holarctic to northern Mexico (Map 3D) ..... *conica*

– Fourth coxa without macrosetae; terminal apophysis filamentous (A in Fig. 39) or hidden behind cymbium (at 3h in Fig. 375) 2

2(1). Conductor tooth broken off (Figs. 411, 412); widespread (Map 8B) ..... *diversa*

– Conductor tooth present 3

3(2). Conductor tooth saber-like, almost half length of conductor or longer (Figs. 82, 84, 93, 94, 374, 376, 408) 4

– Conductor tooth small (Figs. 39, 41, 103) 8

4(3). Tooth shorter than half length of conductor (Figs. 82–85); widespread (Map 4C) ..... *rubronigra*

– Tooth longer than half length of conductor (Figs. 93, 94, 374, 385, 409, 410) 5

5(4). Conductor projecting beyond tegulum (Figs. 374–376) 6

– Conductor not projecting beyond tegulum (Figs. 93, 94, 407, 408) 7

6(5). Median apophysis with lobe as long as wide (Fig. 377); widespread (Map 8A) ..... *bifurcata*

Median apophysis lobe wider than long (Fig. 386); Costa Rica (Map 8B) ..... *jose*

7(5). Conducter tooth gracefully curved, S-shape in apical view (Fig. 94); widespread (Map 4A) ..... *inca*

– Conducter tooth straight to slightly curved (Figs. 407, 409); widespread (Map 8B) ..... *diversa*

8(3). Median apophysis with upright tooth on its inner margin (Figs. 360, 362); Argentina, Chile (Map 6E) ..... *serena*

Median apophysis without such tooth (Figs. 39, 342, 352) 9

9(8). Median apophysis with rows of denticles forming a triangle as in Figures 135, 137; northern Colombian mountains (Map 3A) ..... *nevada*

Median apophysis otherwise 10

10(9). Conductor tooth thin or only a sliver visible above flap (Figs. 103, 106, 114, 143) 11

– Conductor tooth almost as wide as long, parrot beak-shaped (Figs. 41, 159, 173, 177) 22

11(10). Median apophysis with a barb on inner margin (Figs. 39, 153, 320, 343) 16

– Median apophysis without barb (Figs. 172, 194) 12

12(11). Conductor tooth wide (Fig. 143); conductor flap thick, sclerotized (Fig. 144); anterior margin of median apophysis with two overlapping ridges (Fig. 145); Depto. Cundinamarca, Colombia (Map 4E) ..... *pedropalo*

– Conductor tooth narrower (Figs. 103, 300); conductor flap thin, soft (Figs. 106, 301); median apophysis otherwise (Figs. 105, 107) 13

13(12). Lobe of median apophysis asymmetrical, separated by its width from distal tooth (Figs. 107, 302, 303) 14

– Median apophysis otherwise (Figs. 231, 247) 15

14(13). Notch of conductor short and narrow with parallel sides (at 3h in Fig. 301); southern Brazil (Map 5B) ..... *espumoso*

– Notch of conductor wide (Fig. 104); Mexico to northern Argentina (Map 4B) ..... *fililineata*

15(13). Median apophysis with gap between lobe and distal tooth (Fig. 231); Peruvian Amazon area (Map 5C) ..... *dianasilvae*

– Edge of median apophysis lobe continuous with tooth (Fig. 247); Peruvian Andes (Map 5C) ..... *picchu*

16(11). Median apophysis with lobe and tooth (Fig. 312, 332) 17

– Median apophysis with keel on anterior margin (Fig. 321) 18

17(16). Abdomen with one posterior tubercle, or oval in outline (Fig. 309); Costa Rica to Panama (Map 6B) ..... *monteverde*

– Abdomen with three posterior tubercles (Fig. 329); California to Peru (Map 7B) ..... *berlandi*

18(16). Notch of conductor with two curved parallel sides (at 4h in Fig. 152); Bogota, Colombia (Map 4D) ..... *santafe*

– Notch of conductor otherwise (Figs. 319, 341, 351) 19

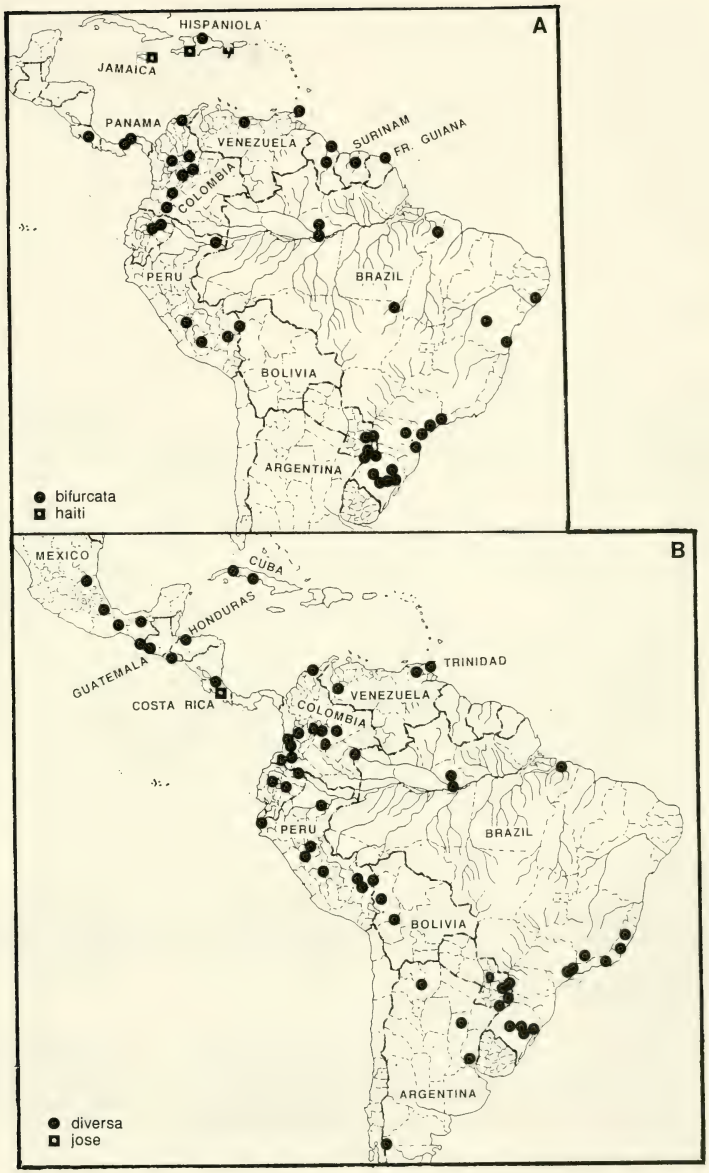
19(18). Abdomen as long as wide (Fig. 349); Baja California (Map 7A) ..... *pichilinque*

– Abdomen longer than wide (Figs. 317, 339) 20

20(19). Conductor lobe encircling tip of tooth and gutter (Fig. 342) 21

– Conductor lobe short (Fig. 116); southern Colombia to northern Ecuadoran Andes (Map 3B) ..... *andinas*

21(20). Abdomen with median extension (Fig. 317); United States to Panama, Ber-



Map 8. Distribution of *Cyclosa* species.

muda, Greater Antilles, Galapagos (Map 6A) ..... *turbinata*

– Abdomen with three posterior tubercles (Fig. 339); Florida, southern Texas and Guiana, West Indies (Map 7A) ..... *walckenaeri*

22(10). Abdomen spherical (Fig. 290); Amazon area (Map 3B) ..... *vicirae*

– Abdomen longer than wide (Fig. 122) ... 23

23(22). Median apophysis with gap between lobe and distal tooth (Fig. 126); Amazon, western Peru to northern Argentina (Map 3A) ..... *longicauda*

– Median apophysis with lobe and tooth adjacent (Figs. 172, 194) 24

24(23). Conductor lobe projecting midway above length of tooth, (arrow on Fig. 173; Fig. 177); wide notch in apical view (Figs. 175, 179); median apophysis tooth as long as height of lobe (Fig. 172); widespread (Map 5D) ... *caroli*

– Conductor lobe and median apophysis otherwise (Figs. 192, 194, 281) 25

25(24). Conductor notch with acute angle at end (Fig. 220); southeastern Brazil (Map 5B) ..... *teresa*

– Conductor notch otherwise (Figs. 160, 282) 26

26(25). Conductor tooth round, median apophysis with small tooth (Figs. 281, 283); Mexico, Lesser Antilles, Venezuela to Peru (Map 6D) ..... *triquetra*

– Conductor tooth (Figs. 253, 261, 271) and median apophysis otherwise (Figs. 264, 274) 27

27(26). Conductor notch about three times as long as wide with parallel sides (Fig. 192); median apophysis with small distal tooth (Fig. 194); widespread from Panama to northern Argentina (Map 5A) ..... *tapetifaciens*

– Conductor notch (Figs. 254, 272) and median apophysis otherwise (Figs. 264, 274) 28

28(27). Conductor notch wide, spreading (Fig. 262); median apophysis tooth behind lobe, pointing proximally (Figs. 263, 264); southern Brazil (Map 6G) *morretes*

– Conductor notch with sides parallel (Figs. 254, 272); median apophysis otherwise (Figs. 161, 255, 273) 29

29(28). Median apophysis tooth pointing toward gutter (Fig. 161); southern Colombia (Map 4D) ..... *huila*

– Median apophysis tooth with greater curvature, pointing backwards (Figs. 255, 273) 30

30(29). Conductor notch narrow, twice as long as wide (Fig. 272); southern Brazil (Map 6C) ..... *machadinho*

– Conductor notch wider, 1.5 times as long as wide (Fig. 254); Pantanal, Mato Grosso (Map 6G) ..... *pantanal*

Cyclosa conica (Pallas)
Figures 42–48; Map 3D

Aranea conica Pallas, 1772: 48, pl. 1, fig. 16. Female specimen from Germany, believed lost.

Cyclosa conica:—Levi, 1977: 78, pl. 1, figs. 1–19, ♀, ♂, map 1.

Variation. Total length of females 3.6 to 7.9 mm, males 3.5 to 4.9.

Diagnosis. The species is easily distinguished from all other Mexican and neotropical *Cyclosa* by the more heavily sclerotized genitalia, by having the scape annulate (Figs. 42, 44), having a sclerotized lobe on each side of the epigynum bent toward the scape (Figs. 42, 44) and by having the terminal apophysis in the palpus in

→

Figures 23–30. *Cyclosa* morphology. 23–25, female of *C. tapetifaciens*. 23, eye region and chelicerae. 24, carapace. 25, carapace and chelicera, lateral. 26, carapace and chelicerae of *C. bifurcata*, lateral. 27–30, male of *C. tapetifaciens*. 27, eye region, chelicerae and right palpus. 28, carapace. 29, carapace and chelicera, lateral. 30, anterior of left second patella and tibia of of male.

Figures 31–37. Epigynum, diagrammatic. 31, ventral. 32, posterior. 33, lateral. 34, 35, *C. nevada* with broken embolus. 34, ventral. 35, posterior. 36, 37, *C. fililineata* with broken embolus. 36, ventral. 37, Dorsal.

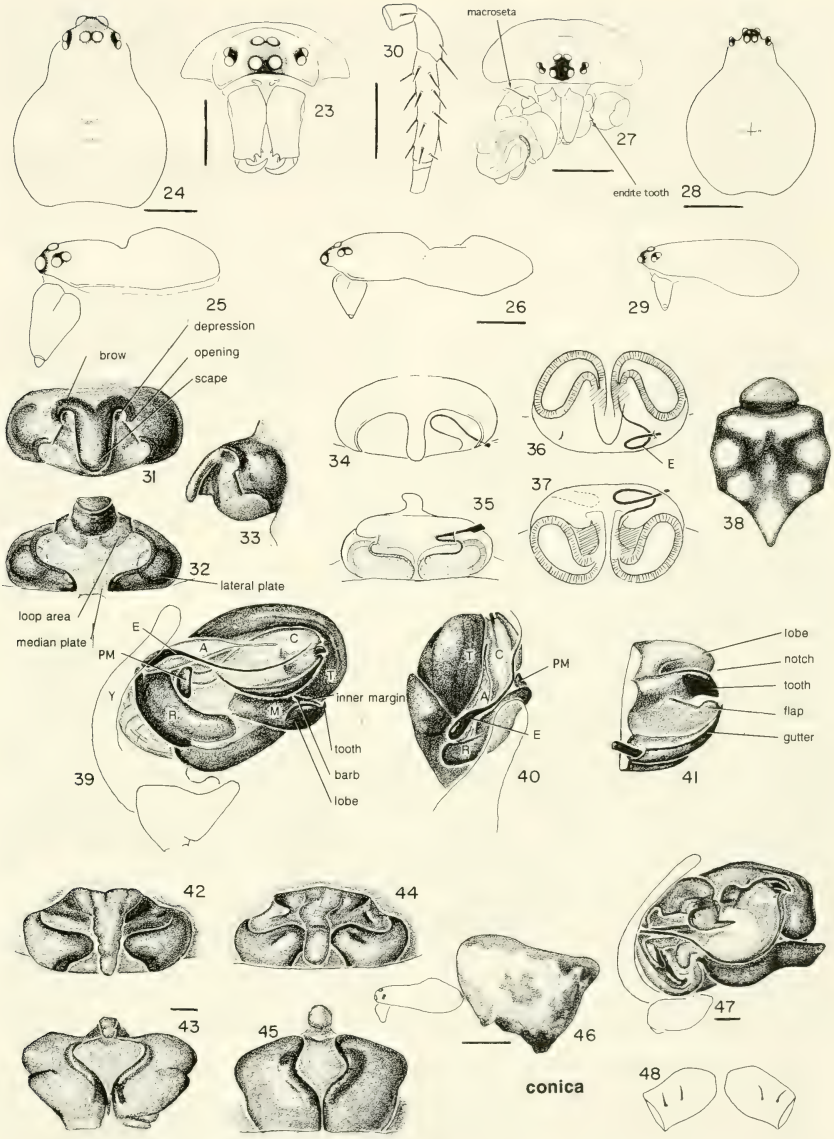
Figure 38. Sternum maculation, *C. walckenaeri*.

Figures 39–41. Male left palpus. 39, mesal, expanded. 40, dorsal, expanded. 41, tip of conductor, pulled apart, diagrammatic.

Figures 42–48. *Cyclosa conica* (Pallas). 42–46, female. 42–45, epigynum. 42, 44, ventral. 43, 45, posterior. 42, 43, (New Hampshire). 44, 45, (Baja California). 46, lateral. 47, 48, male. 47, left male palpus. 48, fourth coxae.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; PM, paramedian apophysis; R, radix; T, tegulum; Y, cymbium.

Scale lines: 1.0 mm; genitalia 0.1 mm.


macroseta
endite tooth
depression
brow
opening
scape
lateral plate
loop area
median plate
inner margin
tooth
barb
lobe
notch
flap
gutter
conica

the shape of an upside-down duck head and torso (A at 10h in Fig. 47). All other *Cyclosa* in Mexico and the neotropics have a transparent rod as terminal apophysis or seem to lack the structure entirely.

Natural History. See Levi, 1977: 79.

Distribution. Holarctic, common in America from Alaska to West Virginia, southern Illinois to southern New Mexico and Baja California (Map 3D).

Specimens Examined. MEXICO *Baja California Norte*: Isla San Lorenzo, north end, 28°40'N, 112°52'W, 24 June 1921, 1♀ (J. C. Chamberlin, CAS).

Cyclosa imias new species
Figures 49–52; Map 3D

Holotype. Female holotype from mountains north of Imias, 3,000–4,000 ft [900 to 1,200 m], Guantánamo Prov., Cuba, 25–28 July 1936 (P. J. Darlington), in MCZ. The specific name is a noun in apposition after the locality.

Note. Bryant and Archer determined specimens of this species as *C. caroli*.

Description. Female holotype. Carapace light brown. Abdomen venter black with a pair of white spots and some median white spots posteriorly. Abdomen with a minute pair of anterior dorsal tubercles and a median posterior extension (Figs. 51, 52). Total length 3.8 mm. Carapace 1.17 mm long, 0.84 wide in thoracic region, 0.53 wide behind posterior lateral eyes. First femur 0.93 mm, patella and tibia 1.04, metatarsus 0.53, tarsus 0.39. Second patella and tibia 0.98 mm, third 0.57, fourth 0.94. Femora shorter than corresponding patellae and tibiae.

Variation. Total length of females 3.8 to 4.2 mm. The illustrations were made from the holotype.

Diagnosis. Cyclosa imias differs from *C. caroli* by having a narrow scape with a wide depression on each side (Fig. 49).

Distribution. Southeastern Cuba (Map 3E).

Specimens Examined CUBA *Santiago de Cuba*: Gran Piedra, 29 June 1955, 4♀ (A. F. Archer, AMNH).

Cyclosa jalapa new species
Figures 53–56; Map 3E

Holotype. Female holotype from Jalapa, Veracruz, Mexico, July 1981 (C. Gold), in CAS. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace brown, cephalic region yellow (Fig. 55). Abdomen venter with white, gray and black areas, and a pair of white patches on tubercles. Abdomen sometimes with a pair of indistinct posterior lateral tubercles (Fig. 55). Total length 5.3 mm. Carapace 1.8 mm long, 1.4 wide in thoracic region, 0.8 wide behind posterior lateral eyes. First femur 1.6 mm, patella and tibia 1.8, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.5 mm, third 0.9, fourth 1.6. Femora shorter than corresponding patellae and tibiae, except for third, which is of same size.

Variation. Total length of females 3.9 to 5.3 mm. The illustrations were made from female holotype.

Diagnosis. Cyclosa jalapa differs from others by the relatively posterior position of the brow and depressions of the epigynum (Fig. 53) and from *C. imias* by the larger posterior median plate (Fig. 54).

Distribution. Known only from Veracruz, Mexico (Map 3E); no other specimens have been collected.

Cyclosa conigera F. P.-Cambridge
Figures 57–61; Map 3E

Cyclosa conigera F. P.-Cambridge, 1904: 494, pl. 47, fig. 5, ♀. Ten female syntypes from Omilteme [Omiltemi, Guerrero, 16 km SW Chilancingo, 17°30'N, 99°40'W (Selander and Vaurie, 1962)],

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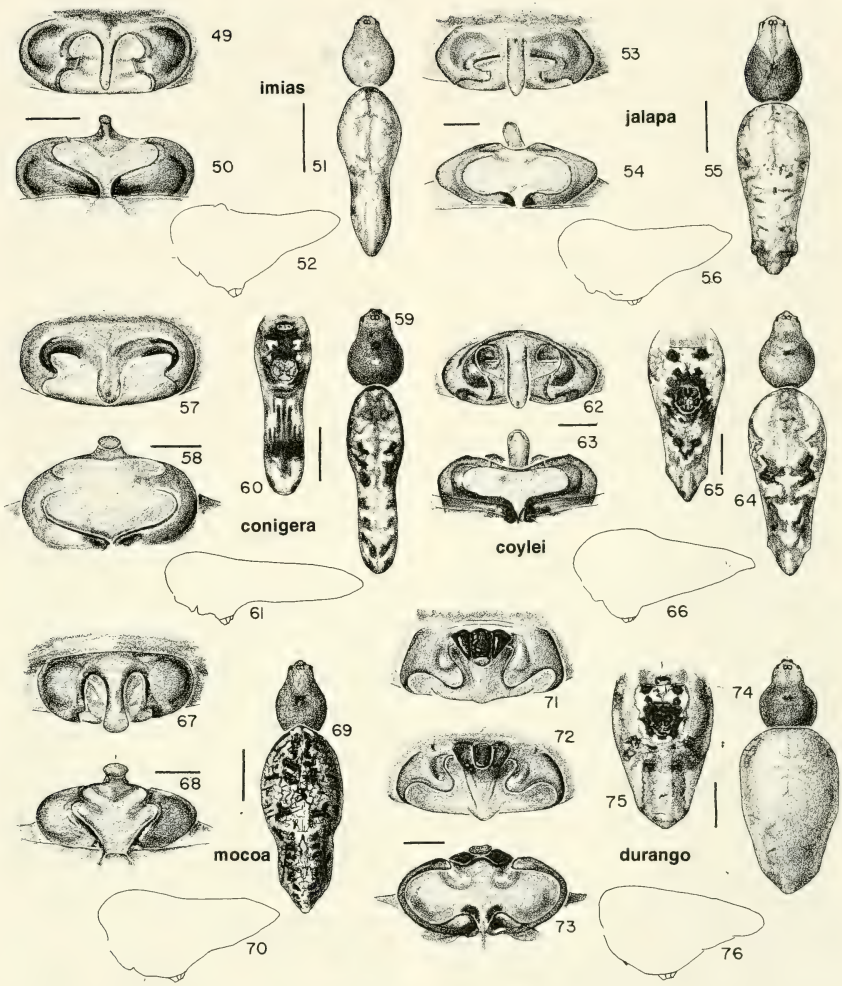
Figures 49–52. *Cyclosa imias* n. sp., female. 49, 50, epigynum. 49, ventral. 50, posterior. 51, dorsal. 52, abdomen lateral.

Figures 53–56. *C. jalapa* n. sp., female. 53, 54, epigynum. 53, ventral. 54, posterior. 55, dorsal. 56, abdomen lateral.



Figures 57–61. *C. conigera* F. P.-Cambridge, female. 57, 58, epigynum. 57, ventral. 58, posterior. 59, dorsal. 60, abdomen, ventral. 61, abdomen, lateral.

Figures 62–66. *C. coylei* n. sp., female. 62, 63, epigynum. 62, ventral. 63, posterior. 64, dorsal. 65, abdomen, ventral. 66, abdomen, lateral.

Figures 67–70. *C. mocoa* n. sp., female. 67, 68, epigynum. 67, ventral. 68, posterior. 69, dorsal. 70, abdomen lateral.

Figures 71–76. *C. durango* n. sp., female. 71–73, epigynum. 71, ventral. 72, ventroposterior. 73, posterior. 74, dorsal. 75, abdomen, ventral. 76, abdomen, lateral.

Scale lines: 1.0 mm; genitalia 0.1 mm.

Mexico in BMNH, not numbered, examined. Roewer, 1942: 759. Bonnet, 1956: 1315.

Note. The name *conigera* was erroneously synonymized with *caroli* by Levi (1977).

Description. Female syntype. Carapace dark brown, lightest in cephalic region (Fig. 59). Sternum dark brown with ring of connected white patches. Coxae yellowish. Legs yellowish with narrow dark rings. Abdomen venter black and white (Fig. 60). Abdomen pointed posteriorly with an indistinct pair of swellings near posterior end (Figs. 59–61). Total length 6.2 mm. Carapace 1.9 mm long, 1.4 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.7 mm, patella and tibia 2.0, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.7 mm, third 1.0, fourth 1.7. All femora shorter than corresponding patellae and tibiae.

Variation. Total length of females 5.4 to 6.2 mm. The illustrations were made from specimens from Mexico.

Diagnosis. Cyclosa conigera differs from *C. rubronigra* (Fig. 77) by the wider brows and depression of the epigynum (Fig. 57) and from *C. dianasilvae* (Figs. 223, 224) by a smaller posterior median plate (Fig. 58). Also *C. dianasilvae* has a short, wide abdomen (Figs. 225–227), whereas the abdomen of *C. conigera* is slender (Figs. 59–61).

Natural History. Specimens have been found in rain forest in Chiapas, Mexico.

Distribution. Mexico to Honduras (Map 3E).

Specimens Examined. MEXICO. *San Luis Potosí*: Ixlitla [probably Xilitla, Mexico], 2 Dec. 1939, 1♀ (A. M., L. I. Davis, AMNH). *Michoacan*: 1.1 mi E Angahuan, 7,500 ft, 14 Aug. 1967, 1♀ (R. E. Leech, REL). *Chiapas*: Selva del Ocote, 32 km NW Ocozocoautla, 762 m, 1♀ (C. Mullinex, D. E. Breedlove, CAS). HONDURAS *Atlántida*: Lancetilla, July 1929, 4♀ (A. M. Chickering, MCZ).

Cyclosa coylei new species
Figures 62–66; Map 3E

Holotype. Female from 4.1 mi. [6.5 km] W of San Francisco on Route 70, 2,400 m, San Luis Potosí, Mexico, 26 May 1982 (F. Coyle) in MCZ. The species is named after the collector and colleague F. Coyle.

Description. Female holotype. Carapace dark brown, lightest in cephalic region (Fig. 64). Abdomen venter black and white (Fig. 65). Abdomen pointed with an indistinct pair of humps near posterior end (Fig. 64). Total length 6.6 mm. Carapace 1.9 mm long, 1.4 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.7 mm, patella and tibia 2.0, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.7 mm, third 1.0, fourth 1.7. The third femur the same length as corresponding patella and tibia, other femora shorter.

Variation. Total length of females 6.1 to 7.2 mm. The illustrations were made from the female holotype. The Guatemalan specimen has a pair of distinct, posterior lateral humps on the abdomen.

Diagnosis. Cyclosa coylei is distinguished from other *Cyclosa* species in Mexico and Guatemala by the large wide and deep depressions of the epigynum (Fig. 62) and the relatively short posterior median plate (Fig. 63).

Natural History. The Guatemalan specimen was found by beating foliage at a river.

Distribution. Mexico, Guatemala (Map 3E).

Specimens Examined. MEXICO *Michoacan*: 1.8 km E Angahuán, 2,200 m, 14 Aug. 1967, 1♀ (R. E. Leech, REL); 9.6 km N Cheran, 7–8 July 1985, 1♀ (J. Woolley, G. Zolnerowich, AD, MCZ). GUATEMALA *Jalapa*: Mataquescuintla, El Carrizal, 25 Apr. 1982, 1♀ (S. Fend, DU).

Cyclosa mocoa new species
Figures 67–70; Map 4A

Holotype. Female holotype, and one female paratype from between Buenos Aires and El Mirador nr. El Silencia, Pasto to Mocoa Road, east slope of Andes, 2,200 m, Depto. Putumayo, Colombia, 1973 (N. Leist), in SMNK. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown (Fig. 69). Abdomen white with symmetrical, finely dissected dark patches

and lines dorsally, (Fig. 69); venter black with a pair of white patches, each longer than wide. Abdomen with a median posterior extension (Figs. 69, 70). Total length 5.3 mm. Carapace 1.5 mm long, 1.0 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.4 mm, patella and tibia 1.5, metatarsus 0.8, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.7, fourth 1.3. Femora shorter than corresponding patellae and tibiae except third, which is of same length.

Variation. The paratype has the scape with the sides more parallel than in Figure 67.

Diagnosis. *Cyclosa mocoa* differs from other species by the elongate depressions (Fig. 67) and the triangular posterior median plate (Fig. 68) of the epigynum.

Distribution. Known only from southern Colombian Andes (Map 4A); no other specimens were found.

Cyclosa durango new species
Figures 71–76; Map 3D

Holotype. Female holotype from 10 mi. (16 km) E of El Salto, Durango, Mexico, 8 Aug. 1947 (W. J. Gertsch), in AMNH. The specific name is a noun in apposition after the locality.

Description. Female holotype. Thoracic region of carapace dark brown grading into yellowish cephalic region (Fig. 74). Abdomen venter with black spinneret area and two pairs of black patches on white between this area and genital region (Fig. 75). Abdomen pointed behind, but specimen shrivelled (Figs. 74–76). Total length 6.0 mm. Carapace 1.8 mm long, 1.3 wide in thoracic region, 0.8 wide behind posterior, lateral eyes. First femur 1.8 mm, patella and tibia 2.0, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.8 mm, third 1.0, fourth 1.7. First femora shorter than corresponding patellae and tibiae, others of same length.

Note. This species is puzzling as no others were found with similar, sclerotized, broken epigynum (at 12h in Fig. 71). It is not known whether the dark structures on each side of the epigynum belong to the spider or are broken conductor teeth left by a male.

Diagnosis. No other species were found having a sclerotized scape of the epigynum (Figs. 71, 72), and no others in Mexico with a large posterior median plate (Fig. 73).

Distribution. Known only from Durango, Mexico (Map 3D); no other specimens were found.

Cyclosa rubronigra di Caporiacco
Figures 77–85; Map 4C

Cyclosa rubronigra di Caporiacco, 1947: 24. Male holotype from Canaira Road [?Kanaima?] (di Caporiacco, 1948), Guyana, in MZUF, examined. Brignoli, 1983: 266.

Cyclosa nigrorubra:—di Caporiacco, 1948: 655, fig. 62, ♂ (error in name).

Description. Female from Panama. Carapace dark brown (Fig. 79). Abdomen venter with black and white patches. Abdomen with a median, posterior extension (Figs. 79, 80). Total length 4.4 mm. Carapace 1.5 mm long, 0.9 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.2 mm, patella and tibia 1.4, metatarsus 0.8, tarsus 0.5. Second patella and tibia 1.2 mm, third 0.7, fourth 1.3. First two femora shorter than corresponding patellae and tibiae, the third and fourth the same length or slightly longer.

Male from Panama. Coloration darker than in female. Abdomen shorter than in female (Fig. 81). Total length 2.5 mm. Carapace 1.43 mm long, 1.01 wide in thoracic region, 0.39 wide behind posterior lateral eyes. First femur 1.06 mm, patella and tibia 1.19, metatarsus 0.75, tarsus 0.35. Second patella and tibia 1.01 mm, third 0.62, fourth 1.04. First two femora shorter than corresponding patellae and tibiae, others of same length.

Note. Two collections had females and males together.

Variation. Total length of females 3.5 to 5.2 mm, males 2.1 to 3.8. The illustrations were made from specimens from Barro Colorado Island, Panama.

Diagnosis. *Cyclosa rubronigra* has

smaller depressions (Fig. 77) than the more northern *C. conigera* (Fig. 57). The female is distinguished from the similar *C. inca* (Fig. 87) by having a slightly smaller posterior median plate (Fig. 78); the male has a shorter conductor tooth (Fig. 83) than that of *C. inca* (Fig. 94).

Distribution. Costa Rica to Rio Grande do Sul, Brazil (Map 4C).

Specimens Examined. COSTA RICA *Heredia*: Finca La Selva, Jan. 1978, 1♂ (W. Eberhard, MCZ); Sept., Oct. 1981, 1♂; 1–14 Oct. 1981, 1♂ (C. Griswold, CAS). *Cartago*: Turrialba, 13 Mar. 1967, 1♂ (W. Peck, CAS). *Puntarenas*: Llorona, Parque Nacional Corcovado, Osa Peninsula, 15 Aug. 1978, 1♀ (Y. D. Lubin, MCZ). PANAMA *Panamá*: Barro Colorado Island, 2 Aug., 1♀, 3 imm. (N. Banks, MCZ), 16 June–15 July 1934, 1♂; June 1936, 1♀; July 1936, 1♂; Aug. 1936, 1♂; Aug. 1939, 1♀; Aug. 1954, 1♀ (A. M. Chickering, MCZ); 13 Sept. 1982, 2♀; 23 Sept. 1982, 1♂; 26 Sept. 1982, 2♀; 28 Oct. 1982, 1♀ (C. L. Craig, MCZ); Experimental Gardens, 5 July 1950, 1♂; 12 Aug. 1954, 1♀ (A. M. Chickering, MCZ); Forest Reserve, 25 July 1954, 1♀ (A. M. Chickering, MCZ); Summit, 21–29 July 1950, 1♂ (A. M. Chickering, MCZ); Arraiján, July 1950, 1♂ (A. M. Chickering, MCZ). LESSER ANTILLES *Trinidad*: Arima Valley, Simla Research Sta., 31 Jan. 1984, 1♀, 1♂ (J. Coddington, USNM); Blanchisseuse Road, St. George, 6 Feb. 1984, 1♀ (J. Coddington, USNM).

VENEZUELA *Bolívar*: 12 km N Luepa, 1,500 m, 1–11 June 1987, 1♂ (S., J. Peck, AMNH). COLOMBIA *Meta*: Carimagua, 100 m, Oct. 1973, 1♀ (W. Eberhard, MCZ). *Valle*: Anchicaya, 400 m, many collections (W. Eberhard 570, MCZ); Cent. Anchicaya, 1♀ (W. Eberhard 845, CAS, MCZ); E of Buenaventura, 20 Jan. 1970, 1♀ (W. Eberhard 226, MCZ); Cali, 1976, 1♂ (W. Eberhard, MCZ); km 18, road to Cali from Saladito, Sept. 1975, 1♂ (W. Eberhard 977, MCZ); Centr. Hidroelectric., Cali, 1♀ (W. Eberhard, MCZ); N Cisneros, Apr. 1976, 1♀ (W. Eberhard 1088, MCZ); El Silencio, 2,000 m, July 1974, 1♀ (W. Eberhard CES-23, MCZ); NW Guapi, 13 Jan. 1973, 1♀ (W. Eberhard, MCZ); nr. Queremal, 19 June 1970, 1♀ (W. Eberhard 282, MCZ); Saladito, Sept. 1974, 1♀ (W. Eberhard 28, MCZ); Mar. 1975, 1♀ (W. Eberhard 946, MCZ); Río San Juan afl., del Digua nr. Queremal, 1,300 m, 1976, 4♀, 1♂ (W. Eberhard 963, MCZ). *Cauca*: Pacific coastal plain, NW of Guapi, Jan. 1973, 1♀ (W. Eberhard, MCZ); 10 km N Piendano, 5,800 m, Feb. 1974, 1♀ (W. Eberhard EG 85, MCZ). *Nariño*: Barbacoa, 20 m, 20 Mar. 1974, 1♀ (W. Eberhard 746, MCZ); Reserva Río Nambi Altaquer, 1,300 m, Oct. 1994, 5♀ (C. Valderrama, CV, MCZ); La Planada, 1,800 m, 7 km S Chocones, July 1986, 1♀, 1♂ (W. Eberhard, MCZ); El Diviso, Aug. 1994, 3♀ (C. Valderrama, CV); La Espriella, 50–60 m, Aug. 1994, 3♀ (C. Valderrama, CV). ECUADOR *Sucumbíos*: Reserva Forestal Cuyabeno, Laguna Grande, 13 Feb. 1989, 1♀ (L. Avilés, MECN). *Pastaza*: Puyo, 18 Apr. 1958, 1♂ (P. W. Hodges, MCZ). PERU *Huánuco*: El Castillo, 2 June 1967, 1♂ (A. F. Archer, S. Risco, AMNH). *Junín*: Maraynioc, 1♂ (K. Jelski, PAN). *Madre de Dios*: Zona Reservada de Manu, Puesta de Vigilancia Pakitza, 24 Sept.–10 Oct. 1987, 1♂ (J. Coddington, USNM). BRAZIL *Pará*: Belém, 12 Feb. 1959, 1♂ (A. M. Nadler, AMNH). *Amazonas*: Reserva Cabo Frío, 80 km N Manaus, 1989–1992, 1♀ (H. G. Fowler, MCZ); Manaus, Reserva Ducke, 23 Feb. 1982, 1♂ (A. A. Lise, MCP 2566). *Goiás*: Goiânia, banks of Rio Meia Ponte, 18 June 1942, 1♀ (F. Lane, MZSP 7288). *Mato Grosso*: Sinop, Oct. 1976, 1♂ (M. Alvarenga, AMNH). *Rio Grande do Sul*: Viamão, 12 Aug. 1994, 1♀ (A. A. Lise, MCP 5277).

Cyclosa inca new species
Figures 86–95; Map 4A

Holotype. Male holotype, female allotype, from Dantas, SW of Puerto Inca, 270 m, 09°38′S, 75°00′W, Huánuco, Peru, 18 May–1 June 1987 (D. Silva), in MUSM. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace yellowish, gray on each side of thorax (Figs. 88, 89). Sternum yellow, gray on margin. Abdomen venter black with a pair of white patches (Fig. 90). Abdomen with median posterior extension, without dorsal tubercles (Figs. 88–90). Total length 3.3

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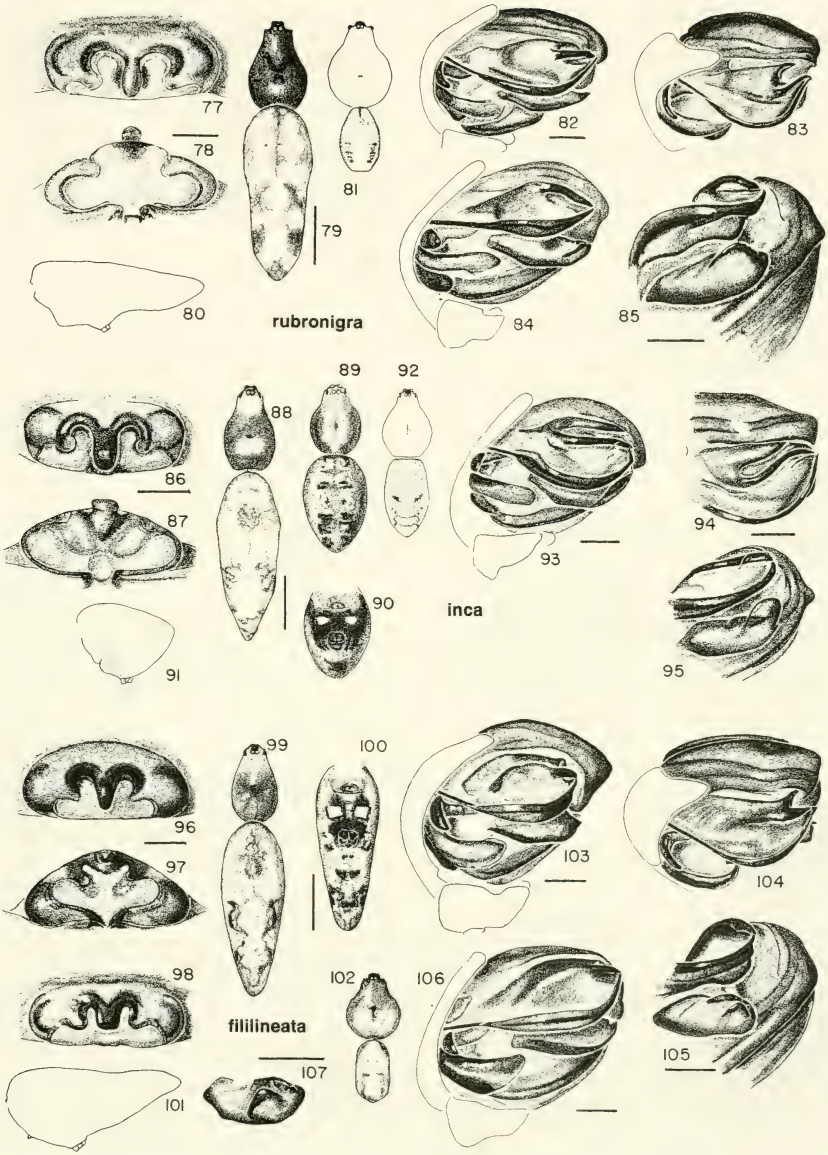
Figures 77–85. *Cyclosa rubronigra* di Caporiacco. 77–80, female. 77, 78, epigynum. 77, ventral. 78, posterior. 79, dorsal. 80, abdomen, lateral. 81–85, male. 81, dorsal. 82–85, left palpus. 82, 84, mesal. 83, apical. 85, median apophysis. 82–83, 85, (Panama). 84, (near Manaus, Brazil).

Figures 86–95. *C. inca* n. sp. 86–91, female. 86, 87, epigynum. 86, ventral. 87, posterior. 88, 89, dorsal. 90, abdomen, ventral. 91, abdomen, lateral. 92–95, male. 92, dorsal. 93–95, palpus. 93, mesal. 94, apical. 95, median apophysis.

Figures 96–107. *C. fililineata* Hingston. 96–101, female. 96–98, epigynum. 96, ventral. 97, posterior. 98, ventral, broken embolus? (Paraná, Brazil). 99, dorsal. 100, abdomen, ventral. 101, abdomen, lateral. 102–107, male. 102, dorsal. 103–107, palpus. 103, 106, mesal. 104, apical. 105, 107, median apophysis. 103–105, 107, (Panama). 106, (Northern Venezuela).

Scale lines: 1.0 mm; genitalia 0.1 mm.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mm. Carapace 1.37 mm long, 0.95 wide in thoracic region, 0.42 wide behind posterior lateral eyes. First femur 1.10 mm, patella and tibia 1.43, metatarsus 0.78, tarsus 0.41. Second patella and tibia 1.25 mm, third 0.73, fourth 1.17. Femora shorter than corresponding patellae and tibiae, except for third, which is slightly longer.

Male allotype. Carapace dark brown. Sternum brown with darker border. Abdomen gray with black and white spots (Fig. 92), venter black with one pair of white patches. Abdomen as in female (Fig. 92). Total length 2.8 mm. Carapace 1.43 mm long, 0.99 wide in thoracic region, 0.38 wide behind posterior lateral eyes. First femur 1.20 mm, patella and tibia 1.30, metatarsus 0.75, tarsus 0.47. Second patella and tibia 1.01 mm, third 0.57, fourth 1.07. Femora shorter than corresponding patellae and tibiae, except third slightly longer.

Note. Males and females were collected together.

Variation. The carapace is of variable coloration, yellow, brown, or yellow with brown marks. The scape of the epigynum is of variable width. Total length of females 3.3 to 5.5 mm, males 2.5 to 2.8. All illustrations were made from specimens from Puerto Inca, Huánuco, Peru.

Diagnosis. The female of *Cyclosa inca* differs from that of *C. rubronigra* (Fig. 78) by having a larger posterior median plate (Fig. 87). The male has a relatively longer conductor tooth (Figs. 93, 94), almost half the length of the bulb, while that of *C. rubronigra* (Figs. 82–84) is about a quarter the length of the bulb. Females from Depto. Valle, Colombia are difficult to separate from *C. rubronigra*.

Natural History. Specimens have been collected by fogging canopy in Tambopata, Peru, and from vegetation in Colombia.

Distribution. Upper Amazon of Colombia and Ecuador, south to Rio Grande do Sul Brazil and Misiones Province, Argentina (Map 4A).

Specimens Examined. COLOMBIA *Amazonas*: Acaracuara, 270 m, 1♀ (C. Valderrama, CV). ECUADOR *Sucumbíos*: Reserva Forestal Cuyabeno, July 1989, 2♀ (G. Estévez, MECN). *Imbabura*: Las Cedros Biol Sta., 1,300–1,450 m, 1♀ (D. Dempsey, MCZ). *Pichincha*: Santo Domingo, 22 Aug. 1992, 1♂ (D. Fitzpatrick, W. Piel, MECN). PERU *Loreto*: Jenaro Herrera, 04°45′S, 78°45′W, 26 Aug. 1988, 6♀ (D. Silva, MUSM); Pithecia, 05°11′S, 72°42′W, 14 Aug. 1989, 1♀, 1♂ (D. Silva, MUSM); Río Samiria, 04°43′S, 74°18′W, 31 May 1990, 1♀ (D. Silva, MUSM); Boca del Río Samiria, 04°39′S, 74°21′N, 11 Aug. 1989, 1♀ (D. Silva, MUSM); Cocha Shinguito, 05°08′S, 74°45′W, 7♀ (T. Erwin, D. Silva, MUSM); May 1990, 1♂ (D. Silva, MUSM). *Amazonas*: Alto Río Comaina, Puesto de Vigilancia Paquisha, 850–1,150 m, 21 Oct–3 Nov. 1987, 6♀, 3♂ (D. Silva, MUSM, MCZ); Montenegro, Bagua, 350 m, 29 Sept., 1 Oct. 1963, 1♂ (Herrer, P. Wygodzinsky, AMNH). *Ucayali*: Bosque Nacional A. von Humboldt, Pucallpa, 29 July 1986, 1♀ (D. Silva, MUSM). *Huánuco*: Cucharas, Huallaga Valley, Feb. Apr. 1954, 3♂ (F. Woytkowski, CAS); Cueva de las Lechuzas, Tingo María, 31 May 1967, 3♀ (A. F. Archer, AMNH); Dantas la Molina, SW de Puerto Inca, 09°38′S, 75°00′W, 18 May–1 June 1987, 5♀, 1♂ (D. Silva, MUSM); Monson Valley, Tingo María, 23 Sept. 1954, 1♀ (E. I. Schlinger, E. S. Ross, CAS). *Pasco*: 2 km La Suiza, Chantabamba, 23 June 1986, 1♂ (D. Silva, MUSM); Huancabamba, Quebrada Chispa, NW Iscozacin, 10°10′S, 75°15′W, 26–30 Oct. 1986, 1♀, 1♂ (D. Silva, MUSM). *Junín*: Utcuyacu, 1,600–2,200 m, Mar. 1948, 1♂ (F. Woytkowski, AMNH). *Madre de*

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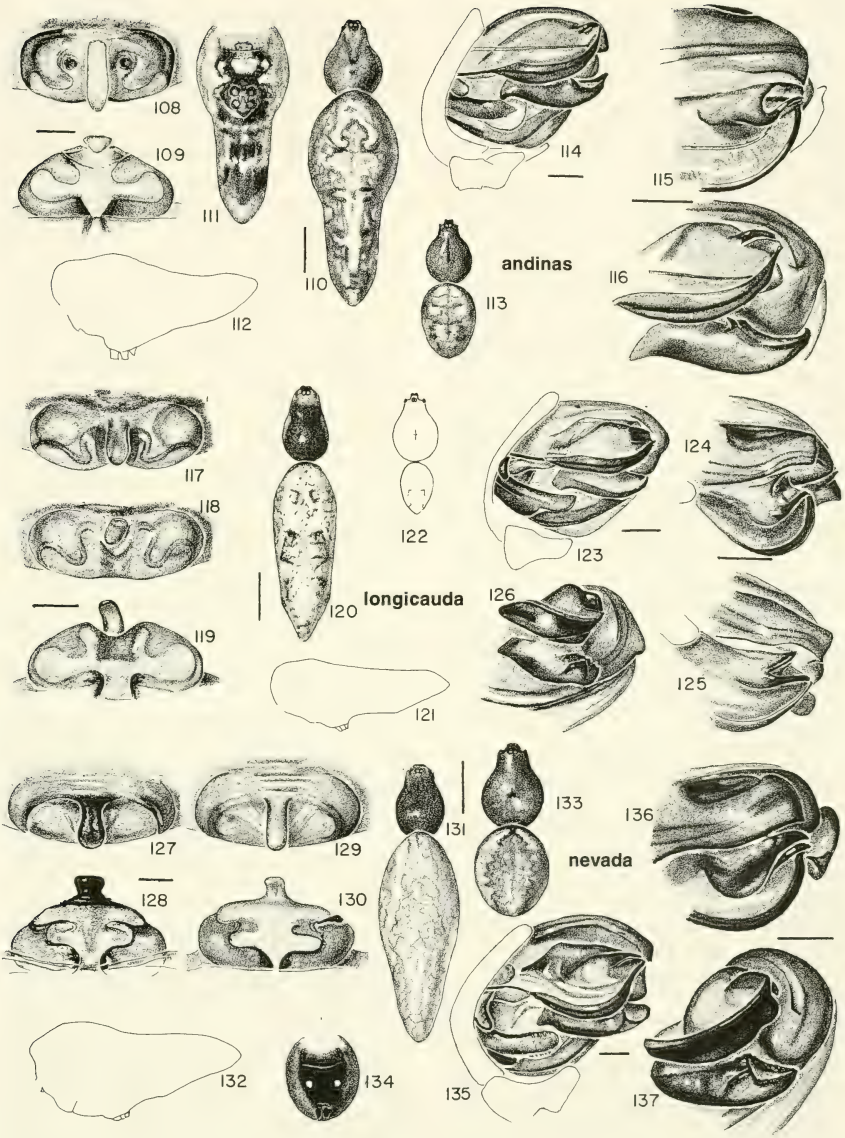
Figures 108–116. *Cyclosa andinas* n. sp. 108–112, female. 108, 109, epigynum. 108, ventral. 109, posterior. 110, dorsal. 111, abdomen, ventral. 112, abdomen, lateral. 113–116, male. 113, dorsal. 114–116, left palpus. 114, mesal. 115, apical. 116, median apophysis.

Figures 117–126. *C. longicauda* (Taczanowski). 117–121, female. 117–119, epigynum. 117, ventral. 118, ventroposterior. 119, posterior. 120, dorsal. 121, abdomen, lateral. 122–125, male. 122, dorsal. 123–126, left palpus. 123, mesal. 125, apical. 126, median apophysis.

Figures 127–137. *C. nevada* n. sp. 127–132, female. 127–130, epigynum (from same coll.). 127, 129, ventral. 128, 130, posterior. 131, dorsal. 132, abdomen, lateral. 133–137, male. 133, dorsal. 134, abdomen, ventral. 135–137, palpus. 135, mesal. 136, apical. 137, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.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Dios: Atalaya, 23 Sept. 1989, 1♂ (D. Silva, MUSM); 13–15 km E Puerto Maldonado, 12°33'S, 69°03'W, 9. 10 June 1989, 1♀, 1♂; 18 July 1989, 1♂ (D. Silva, MUSM); 23 June 1989, 1♀ (D. Silva, MUSM); 9 July 1989, 2♀ (D. Silva, MUSM); Zona Reservada Manu, Pakitza, numerous records (MUSM, USNM); Zona Reservada Tambopata, numerous records (MUSM, USNM); Tambopata Explorer's Inn, 30 Mar. 1988, 1♀ (J. Palmer, D. Smith, MCZ). BRAZIL *Amazonas*: Colosso Reserve, 80 km N Manaus, 1989–1991, numerous collections, ♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ); Dimona Reserve, 1989–1992, 1♀ (H. Fowler, MCZ); Km 41 Reserve, 80 km N Manaus, 18 Apr. 1991, 2♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ); Porto Alegre, 80 km N Manaus, 1989–1992, 1♀ (H. Fowler, MCZ); Cabo Frio Reserve, 1989–1993, 1♂ (H. G. Fowler, MCZ); Parque Nacional do Pico Neblina, Maturacá, 13 Oct. 1990, 1♀ (A. A. Lise, MCP). *Rio Grande do Sul*: Montenegro, 11 Aug. 1977, 2♀, 7 imm. (A. A. Lise, MCN 6285). BOLIVIA *La Paz*: Sepecho [?], 30 July 1993, 1♀ (A. Brescovit, M. Höfer, SMNK 1366) *Beni*: Estacíon Biolo. Beni, 9 Sept. 1987, 1♀ (S. Larcher, USNM); 24, 25 July 1993, 2♀ (A. Brescovit, MCN 24120, SMNK 1370). PARAGUAY *Alto Paraná*: Puerto Stroessner [Ciuded del Este], CFAP, Parcelle iv, Monte Natural, 10 Mar. 1983, 1♂ (C. Dlouhy, MHNG). ARGENTINA *Misiones*: Parque Nacional Iguazú, Jan. 1966, 1♂ (M. E. Galiano, MECN).

Cyclosa fililineata Hingston
Figures 96–107; Map 4B

Cyclosa sericaria Simon, 1895: 782. Nomen nudum.
Cyclosa fililineata Hingston, 1932: 116, 371. Female from Essequibo River, Guyana, in BMNH, lost. Female neotype, here designated, with imm. male from Santarém, Est. Pará, Brazil, 28 Jan. 1994 (A. D. Brescovit) in MCN no. 25340. Roewer, 1942: 759. Bonnet, 1956: 1316.
Cyclosa filisinuosa Hingston, 1932: 114, 372. Male from Essequibo River, Guyana, in BMNH, lost. Roewer, 1942: 759. Bonnet, 1956: 1316. NEW SYNONYMY.

Note. *Cyclosa sericaria* is cited by Simon from San Esteban, Est. Carabobo, Venezuela; a specimen is in the MNHN, but no description could be found.

Hingston describes *C. fililineata* with the abdomen oval, no shoulder humps, posterior end pointed, without tubercles, total length 2.7 mm; *C. fillisinuosa* total length 1.5 mm. Both of Hingston's specimens may have been immature.

Description. Female from Santarém, Pará, Brazil, MCN 25340. Carapace brown, cephalic region yellow (Fig. 99). Abdomen venter black with a large pair of symmetrical white patches (Fig. 100). Abdomen with narrow, posterior extension (Fig. 99), but without dorsal tubercles. Total length 4.7 mm. Carapace 1.43 mm long, 0.91 wide in thoracic region, 0.49 wide behind posterior lateral eyes. First femur 1.11 mm, patella and tibia 1.38, metatarsus 0.78, tarsus 0.45. Second patella and tibia 0.79 mm, third 0.72, fourth 1.18. All femora shorter than corresponding patellae and tibiae.

Male from Santarém, Pará, Brazil, MCN 25295. Carapace much darker than in female, thorax having a light brown transverse area (Fig. 102). Abdomen light with some dark marks, venter black without white patches. Abdomen relatively wide posteriorly (Fig. 102). Total length 2.4 mm. Carapace 1.35 mm long, 1.00 wide in thoracic region, 0.37 wide behind posterior lateral eyes. First femur 1.00 mm, patella and tibia 1.13, metatarsus 0.72, tarsus 0.39. Second patella and tibia 0.95 mm, third 0.48, fourth 0.93. First two femora shorter than corresponding patellae and tibiae, third longer, fourth of same length.

Note. Males and females were collected together.

Variation. Total length of females 3.4 to 5.2 mm, most less than 5 mm; males 2.1 to 2.9. Figures 96, 97, 99–101 illustrate the female neotype; Figure 98 from Ilha Guarani, Paraná, Brazil; Figures 102–104, 107 from from Ilha Arvoredo, Santa Catarina, Brazil; Figures 105, 106 from Aragua, Venezuela.

Diagnosis. The epigynum (Fig. 96) has depressions slightly smaller than those of *C. rubronigra* (Fig. 77) and *C. inca* (Fig. 86) and has a much smaller posterior median plate (Fig. 97) than in *C. rubronigra* (Fig. 78) and *C. inca* (Fig. 87). The palpus differs from these two species by having a smaller, wider conductor tooth (Figs. 103, 106) and the median apophysis with an asymetrical lobe (Figs. 105, 107).

Natural History. This species is smaller than most species of *Cyclosa*. Specimens

have been collected by fogging canopy in Tambopata, Peru; from rainforest at Explorama Inn, Iquitos, Peru; in forest in Belém; and in gallery forest in northern Mato Grosso.

Distribution. Widespread from Panama to northern Argentina (Map 4B).

Specimens Examined. PANAMA *Panamá*: Cerro Galero, ♂ (MCZ). LESSER ANTILLES *Trinidad*: Arima Ward, Blanchisseuse Road, ♀ (USNM). VENZUELA *Aragua*: Rancho Grande, Henri Pittier National Park, 750 m, ♂ (USNM). *Merida*: Merida road to Azulita, La Carbonero, ♀ (MCZ). GUYANA Isherton [?], ♀ (AMNH). FRENCH GUIANA Cayenne, ♂ (AMNH). COLOMBIA *Amazonas*: 48 km NW Leticia, Amacayacu Parque Nacional, ♀ (MCZ); Río Pira and Apaporis, 0°25′S, 70°15′W, ♀ (CAS). ECUADOR *Sucumbíos*: Reserva Forestal Cuyabeno, ♀ (G. Estévez, MECN). *Napo*: Misuagualli, Oriente [Misahualli], ♀ (AMNH). PERU *Loreto*: Explorama Inn, 240 km NE Iquitos, ♀ (FSCA); Jenaro Herrera, 04°45′S, 73°45′W, ♀ (MUSM); Cocha Shinguito, 05°08′S, 74°45′W, ♀♂ (MUSM); Pebas [and São Paulo de Olivença], ♀ (MNHN 40956). *Ucayali*: Bosque Nacional A. von Humboldt, nr. Pucalpa, ♀ (MUSM). *Huánuco*: Dantas, ♀♂ (USNM, MUSM); Monson Valley, Tingo María, ♀♂ (CAS); Tingo María, ♀ (AMNH). *Pasco*: Quebrada Castilla, 10°10′S, 75°15′W, ♀ (MUSM). *Madre de Dios*: Zona Reservada Pakitza, ♀ (MUSM); ♀ (MUSM); 15 km E Puerto Maldonado, ♀ (MUSM). BRAZIL *Pará*: Alter do Cháo, Santarém, ♀ (MCN 25321); Belém, ♀♂ (MACN); ♀ (MCZ); Fazenda Velha, Belém, ♀♂ (MACN); Santarém, Alter do Chão, ♂ (MCN 25295, SMNK); ♀ (MCN 25048, 25584). *Roraima*: Maracá, ♂ (INPA); ♀ (INPA); ♀♂ (INPA); Ilha de Maracá, ♂ (INPA); ♀♂ (MCN 27077, 27080); Rio Uraricoera, ♂ (MCN 27079); ♂ (MCN 27078); ♀ (MCN 27073); ♂ (MCN 27076); ♀♂ (MCP 1884); Ilha de Ularacá, ♂ (INPA); Ularacá, ♀ (INPA). *Amazonas*: Colosso Reserve, ♀♂ (MCZ); Km 41 Reserve, ♀ (MCZ); Manaus, ♀ (MCZ); Manaus, Reserva Ducke, ♀♂ (INPA, MCN 27074, 27075); ♂ (MCN 21406); Tarumã Mirím, flooded forest area nr. Manaus, ♀ (INPA); [Pebas] and São Paulo Olivença, ♀ (MNHN 40956). *Pernambuco*: Pernambuco, ♂ (SMF). *Mato Grosso*: Barra do Tapirape, ♂ (AMNH); Chapada dos Guimaroás, ♀ (MCP 2363, 2167); Chavantina, 1♀ (MZSP 4640); ♀ (MZSP 1202); Poconé, Pantanal, ♂ (MCP 2430); Porto Cereado, ♂ (MCP 2607); Sta. Antonio de Levergere, ♂ (MCZ). *Mato Grosso do Sul*: 30 km de Miranda, Pantanal, ♀ (MCN 25670). *Rio de Janeiro*: Rio de Janeiro, ♀ (MNHN 8509); Teresópolis, 900–1,000 m, ♀ (AMNH); Sumaré, Rio de Janeiro, ♀ (AMNH). *São Paulo*: Amparo, ♀ (MZSP 4635); nr. Botucatu, ♀ (MCZ); Botucatu Vitoriana, Fazenda Edgardia, ♀ (I. M. P. Rinaldi, IMPR); Botucatu, Rubias Junior, ♀ (IMPR); Itu, ♂ (MZSP 9592); Jequirituba, Cidade São Paulo, ♀ (AMNH); Nova Europa, ♀ (MZSP 4335); Fóz do Iguaçu, ♀ (MCN 23491); Rio Clara, ♂ (MZSP 9664); São Roque, ♂ (MZSP 13155); São Sebastião, Barra do Una, ♀ (MZSP 9532). *Paraná*: Almirante Tamandaré, ♂ (MCN 12507); Colombo, ♂ (MCN 20577); Parque Nacional do Iguaçu, Fóz do Iguaçu, ♀♂ (MCN 23345, 23531); Salto Caxias Rio Iguaçu, ♀ (MCZ); ♂ (MCN 23433); Parque Nacional do Iguaçu, Capitão Leonidas Marques, ♀ (MCN 23298); Refúgio Biológico de Bela Vista, Foz de Iguaçu, ♀♂ (MCN 20879); ♀ (MCN 21640); Serra da Graciosa, Morretes, ♀ (MCP 7171); Rancho Queimado [?], ♀ (MCN 25834); Três Barras do Paraná, Rio Guarani, ♀♂ (MCN 22999). *Santa Catarina*: Res. Biológica Arvoredo, ♀ (MCP 7474); Ilha de Arvoredo, ♀♂ (MCP 4052); Estrada Concórdia, 27°11′S, 52°10′W, ♀ (MCN 27241). *Rio Grande do Sul*: Almirante Tamandaré, ♂ (MCN 12405); General Câmara, ♂ (MCN 10734); Irai, ♀ (MCN 3131); Linha Alegre, Arroio do Meio, ♂ (MCN 12902); Machadinho, ♂ (MCN 18938); Montenegro, ♂ (MCN 6239); Parque Florestal Estadual de Nonoai, ♀ (MCN 12814); Paço de Carvão, Campo Bom, ♂ (MCN 9368); Barra do Ouro, Osório, ♂ (MCN 12765); Tenente Portela, ♀ (MCN 8969a); Santa Maria, ♂ (MCN 15301); Santa Maria, Três Barras, ♂ (MCP 4636); Viamão, ♀ (MCP 4671). PARAGUAY *Concepción*: Apo, ♀ (AMNH). *Paraguarí*: Ybycui Natl. Park, ♀ (MCZ). *Alto Paraná*: Taguarazapa, ♀♂ (AMNH). BOLIVIA *La Paz*: Sapecho, Alto Beni, ♀ (MCN 24076). *Beni*: Mamuré "Geb" [Gebiet, Gebirge, area, mountains?], northern Bolivia, ♀ (SMF); Estação Biol. de Beni, ♀♂ (USNM); ♀ (USNM); ♀ (MCN 24129). ARGENTINA *Misiones*: Santa María, ♀ (MACN); Parque Nacional Iguazú, ♀ (MACN); 30 km Puerto Bemberg [Puerto Libertad], Río Urugua-í, ♀ (MACN 3165). *Chaco*: Río de Oro, ♀ (MACN).

Cyclosa andinas new species
Figures 108–116; Map 3B

Holotype. Female holotype, male allotype, five female and two male paratypes and eight immatures from near Habana, 2,200 m elev., on dead end road east of Palmira, Valle, Colombia, 16 Sept. 1969 (W. Eberhard), in MCZ. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace dark brown (Fig. 110). Abdomen with fine black markings (Fig. 110), venter black and white with three white patches in a row between epigynum and spinnerets (Fig. 111). Abdomen narrow pear-shaped (Fig. 112). Total length 5.7 mm. Carapace 1.7 mm long, 1.2 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.6 mm, patella and tibia 1.9,

metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.7 mm, third 0.7, fourth 1.5. Femora shorter than corresponding patellae and tibiae, except third, which is longer.

Male allotype. Carapace dark brown. Abdomen black on each side anteriorly (Fig. 113); venter black with with a pair of distinct white spots. Abdomen drop-shaped (Fig. 113). Total length 3.3 mm. Carapace 1.52 mm long, 1.12 wide in thoracic region, 0.51 wide behind posterior lateral eyes. First femur 1.44 mm, patella and tibia 1.46, metatarsus 0.78, tarsus 0.44. Second patella and tibia 1.20 mm, third 0.68, fourth 1.12. Second to fourth femora slightly longer than corresponding patella and tibia.

Note. Males and females were collected together. This species may be social.

Variation. Total length of females 5.7 to 7.0 mm, males 2.8 to 3.7. The illustrations (Figs. 108–116) were made from female holotype and male allotype.

Diagnosis. The shape of the abdomen (Figs. 110–112) separates *C. andinas* from *C. walckenaeri* (Figs. 337, 338). The narrow scape and deep depressions of the epigynum (Figs. 108, 109) separate the female, and the long, narrow conductor tooth and barb of the median apophysis (Fig. 116) separate the male from similar species.

Natural History. This species lives at high elevation, 2,200–2,400 m elevation, and the collector referred to them as an aggregate.

Distribution. Southern Colombian and northern Ecuadoran Andes (Map. 3B).

Paratypes. Three females and 12 immatures from roadside from type locality.

Specimens Examined. COLOMBIA Marcopampa [?], 2,400 m, 10 Nov. 1973, 7♀, 2♂ (K. Leist, SMNK). *Huila*: 12 km E Santa Leticia [2°20′N, 76°14′W], 2,300 m, Mar. 1976, 1♂ (W. Eberhard, MCZ). *Putumayo*: east slope of Andes, Pasto-Mocoa Road, between Buenos Aires and El Mirador near Silencio, 1973, 1♀ (K. Leist, SMNK). ECUADOR *Pichincha*: Santo Domingo Road, Quito, 2,500 m, 25 Apr. 1942, 1♀, 3♂ (H. F. Haught, CAS).

Cyclosa longicauda (Taczanowski), new combination

Figures 117–126; Map 3A

Singa longicauda Taczanowski, 1878: 145. Female holotype from Amable María [Río Tulumayo valley, W of Tulumayo, ca. 10 km S of San Ramón, 11°10′S, 75°19′W, Depto. Junín (Stephens and Traylor, 1983)], Peru in PAN, examined. Roewer, 1942: 877.

Araneus longicaudus:—Bonnet, 1955: 530.

Description. Female from Quebrada Chispa. Carapace brown, eye region lightest and a yellow band on each anterior margin of thoracic region (Fig. 120). Abdomen white, only lightly marked dorsally with black lines and spots (Fig. 120); venter black with indistinct white patches. Abdomen with a median posterior extension (Fig. 121); the extension of the abdomen from the spinnerets to the posterior tip is twice as long as the abdomen anterior to the median spinnerets (Fig. 121). Total length 5.6 mm. Carapace 1.6 mm long, 1.1 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.4 mm, patella and tibia 1.7, metatarsus 0.9, tarsus 0.6. Second patella and tibia 1.5 mm, third 0.9, fourth 1.5. Femora shorter than corresponding patellae and tibiae, except third, in which it is same length.

Male from Quebrada Chispa. Carapace dark brown. Total length 2.5 mm. Carapace 1.34 mm long, 0.91 wide in thoracic region, 0.39 wide behind posterior lateral eyes. First femur 1.13 mm, patella and tibia 1.18, metatarsus 0.72, tarsus 0.40. Second patella and tibia 0.92 mm, third 0.54, fourth 1.04. Length of first and fourth femora shorter than corresponding patellae and tibiae, second same length, third longer.

Note A male and female were collected together at Quebrada Chispa. One female from Ecuador was collected with a male of *C. inca*.

Variation. Total length of females 3.8 to 5.8 mm. The epigyna with the widest scapes came from Bolivia. The illustrations were made from female and males from Depto. Pasco, Peru.

Diagnosis. Females differ from all other *Cyclosa* without dorsal tubercles on the abdomen (Fig. 121) by having a deep groove underneath the scape of the epigynum (Figs. 117–119). The groove can be seen in posterior view by the median dent along the upper margin underneath the scape (Fig. 119). In subventral view a dark V-shaped mark is visible behind the scape (Fig. 118). The male differs from others by the short, wide, parrot beak-shaped conductor tooth and the asymmetrical median apophysis lobe (Fig. 126).

Distribution. Amazon area, western Colombia, Peru to Misiones Prov., Argentina (Map 3A).

Natural History. Specimens have been collected at night and in a low mudflat, Beni Biol. Station, Bolivia.

Specimens Examined. COLOMBIA *Valle*: 18 km E of Buenaventura, 50 m, 20 Jan. 1970, 1♀ (W. Eberhard, MCZ); nr. Cali, 1,000 m, 1♀ (W. Eberhard E-58, MCZ). ECUADOR *Pichincha*: Santo Domingo, 0°15′S, 79°09′W, 22 Aug. 1992, 1♀ (D. Fitzpatrick, W. Piel, MECN). PERU *Loreto*: Cocha Shinquito, 05°08′S, 74°45′W, 27 June 1990, 7♀ (T. Erwin, D. Silva, MUSM); Pithecia, 05°11′S, 72°42′W, 14 Aug. 1989, 1♀ (D. Silva, MUSM). *Amazonas*: Alto Río Comaina, Puesto de Vigilancia Falso Paquisha, 21 Oct–3 Nov. 1987, 2♀ (D. Silva, MUSM). *Ucayali*: Bosque Nacional A. von Humboldt, 30 July 1986, 1♀ (D. Silva, MUSM). *Huánuco*: Dantas la Molina, SW of Puerto Inca, 18 May–1 June 1987, 3♀ (D. Silva, MUSM). *Pasco*: Huancabamba, Quebrada Chispa, NW de Iscozacin, 345 m, 10°10′S, 75°15′W, 26–30 Oct. 1986, 3♀, 2♂ (D. Silva, MUSM); Quebrada Castilla, NW de Iscozacin, 13 Oct. 1987, 2♀ (D. Silva MUSM); Oxapampa, 22 June 1986, 1♀ (D. Silva, MUSM). *Madre de Dios*: 15 km E Puerto Maldonado, 1 June 1989, 1♀ (D. Silva, MUSM); Zona Reservada Pakitza, 27 Sept. 1987, 1♀ (J. Coddington, D. Silva, MUSM); 1–4 Oct. 1987, 2♀ (D. Silva et al., USNM); 9 May 1991, 1♀ (D. Silva, MUSM); 10–19 Oct. 1991, 1♀ (D. Silva et al., USNM); Zona Reservada Tambopata, 1987–1988, 4♀ (D. Silva, MUSM); Explorers Inn, 30 Mar. 1988, 1♀ (J. Palmer, D. Smith, MCZ). BOLIVIA *Beni*: Estacion Biol. Beni, 27 km SW Yucomo, 17 Sept. 1987, 1♀ (W. E. Steiner et al. USNM); 12 Nov. 1987, 1♀ (W. E. Steiner et al., USNM); 15–19 Nov. 1989, 1♀ (J. Coddington et al., USNM); 27 km SW Tucuma, 15–19 Nov. 1989, 3♀ (J. Coddington et al., USNM). BRAZIL *Amazonas*: Km 41 Reserve, 80 km N Manaus, 1889–1992, 1♀ (H. Fowler, MCN); Cabo Frio Reserve, 80 km N Manaus, 7 Feb. 1990, 1♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ). *Paraná*: Parque Nacional de Iguaçu, Foz de Iguaçu, 29, 30 Mar. 1994, 1♀ (A. B. Bonaldo, MCN 23491a). ARGENTINA *Misiones*: Parque Nacional Iguazú, Sendero Macuco, 6 Oct. 1993, 1♀ (M. Di Vitteti, MACN).

Cyclosa nevada new species
Figures 127–137; Map 3A

Holotype. Female holotype, male allotype, and 14 female and 18 male paratypes from San Lorenzo, Sierra Nevada de Santa Marta, Depto. Magdalena, 2,200 m, in front of building of the nature protection department, Inderana, 18–25 Aug. 1985, Colombia (H.-G. Müller), in SMF. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown, eye region lightest (Fig. 131). Abdomen white with irregular lines and indications of a pair of white bands (Fig. 131); venter with white patches between epigynum and spinnerets. Abdomen with median posterior extension (Fig. 132). Total length 5.8 mm. Carapace 1.3 mm long, 1.0 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.2 mm, patella and tibia 1.5, metatarsus 0.7, tarsus 0.6. Second patella and tibia 1.3 mm, third 0.7, fourth 1.2. Femora shorter than corresponding patellae and tibiae, except third, which is the same.

Male allotype. Coloration as in female, except eye region dark brown. Abdomen with faint indication of a folium (Fig. 133). Abdomen oval with a posterior median tubercle (Fig. 133). Abdomen oval with a posterior median tubercle (Fig. 133). Total length 3.1 mm. Carapace 1.56 mm long, 1.21 wide in thoracic region, 0.52 wide behind posterior lateral eyes. First femur 1.44 mm, patella and tibia 1.66, metatarsus 0.88, tarsus 0.46. Second patella and tibia 1.30 mm, third 0.74, fourth 1.12. Length of femora shorter than corresponding patellae and tibiae, except third, which is longer.

Note. Males and females were collected together.

Variation. Total length of females 4.6 to 6.8 mm, males 2.9 to 3.3. No two specimens have the same length, width or shape of the scape (Figs. 127, 129). The

illustrations were made from holotype and allotype.

Diagnosis. Females are separated by the narrow lateral plates of the epigynum in ventral view (Figs. 127, 129), and the small posterior median plate (Figs. 128, 130); males differ from all other species by the shape of the rows of denticles on the median apophysis (Fig. 137).

Natural History. Females were collected in moist debris and mosses, low growth vegetation, roadside vegetation, pasture with shrubs, and in coniferous forest (*Cupressus* sp.).

Distribution. Northern Colombian Sierra Nevada de Santa Marta (Map 3A).

Specimens Examined. COLOMBIA *Magdalena*: San Lorenzo, Sierra Nevada de Santa Marta, 2,200 m, 18–25 Aug. 1985, 15♀, 23♂ (H. G. Müller, SMF); 20 Apr. 1986, 1♀ (H. G. Müller, SMF).

Cyclosa pedropalo new species
Figures 138–145; Map 4E

Holotype. Female holotype, male allotype and one female, one male paratype from Pedro Palo, 2,000 m elev., Depto. Cundinamarca, Colombia (C. Valderrama), in MCZ, paratypes in ICNB. The specific name is a noun in apposition after the locality.

Note. Pedro Palo is a small pond close to a town named La Mesa, 40 to 50 km west of Bogota (C. Valderrama, personal correspondence).

Description. Female holotype. Carapace dark brown (Fig. 140). Abdomen venter black with white patches. Abdomen with a posterior extension (Fig. 141). Total length 6.0 mm. Carapace 1.9 mm long, 1.2 wide in thoracic region, 0.8 wide behind posterior lateral eyes. First femur 1.6 mm, patella and tibia 1.9, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.7 mm, third 1.0, fourth 1.7. Femora shorter than corresponding patellae and tibiae, except third, which is of equal length.

Male allotype. Coloration similar to that of female, except venter black with pair of white spots. Abdomen as in female (Fig. 142). Total length 4.0 mm. Carapace 1.70 mm long, 1.33 wide in thoracic region, 0.54 wide behind posterior lateral eyes. First femur 1.69 mm, patella and tibia 1.82, metatarsus 0.91, tarsus 0.48. Second patella and tibia 1.43 mm, third 0.80, fourth 1.43. First two femora shorter than corresponding patellae and tibiae, third longer, fourth of equal length.

Note. Males and females were collected together.

Variation. Total length of females 6.0 to 6.7 mm. The illustrations were made from female holotype and male allotype.

Diagnosis. The epigynum is separated from others by the straight lip of the opening (Fig. 138) and the large posterior median plate (Fig. 139). The males have relatively heavy sclerotization of the conductor flap (Figs. 144, 145).

Distribution. Colombian Andes (Map 4E).

Specimens Examined. COLOMBIA *Putumayo*: El Diviso, Pasto to Mocoa road, E slope Andes, ca. 2,000 m, 3 Dec. 1973, 6♀ (N. Leist, SMNK). *Nariño*: La Ceja, on road W side Volcán Chiles, 30 km from town of Chiles, 2,600 m, June 1995, 2♀ (C. Valderrama, CVC).

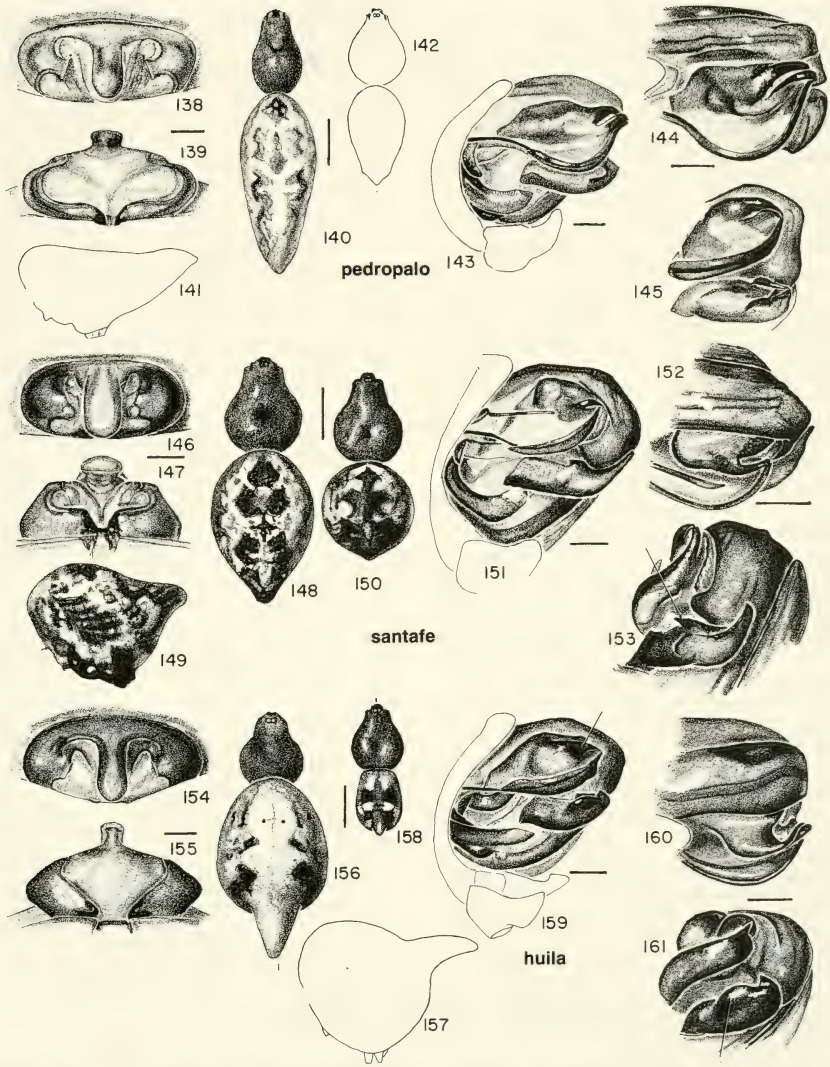
Cyclosa santafe new species
Figures 146–153; Map 4D

Holotype. Female holotype, male allotype from 16 km W Bogota, Colombia, 10 Mar. 1955 (E. S. Ross, E. I. Schlinger), in CAS. The specific name is a noun in apposition after the full name of the locality, Santa Fé de Bogota.

Description. Female holotype. Carapace dark brown (Fig. 148). Abdomen contrastingly marked (Fig. 148); venter black with white patches. Abdomen short with a dorsal posterior extension (Fig. 148). Total length 4.6 mm. Carapace 1.8 mm long, 1.4 wide in thoracic region, 0.8 wide behind

→

Figures 138–145. *Cyclosa pedropalo* n. sp. 138–141, female. 138–139, epigynum. 138, ventral. 139, posterior. 140, dorsal. 141, abdomen, lateral. 142–145, male. 142, dorsal. 143–145, left palpus. 143, mesal. 144, apical. 145, median apophysis.



Figures 146–153. *C. santafe* n. sp. 146–149, female. 146, 147, epigynum. 146, ventral. 147, posterior. 148, dorsal. 149, abdomen, lateral. 150–153, male. 150, dorsal. 151–153, palpus. 151, mesal. 152, apical. 153, median apophysis.

Figures 154–161. *C. huila* n. sp. 154–157, female. 154, 155, epigynum. 154, ventral. 155, posterior. 156, dorsal. 157, abdomen, lateral. 158–161, male. 158, dorsal. 159–161, palpus. 159, mesal. 160, apical. 161, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

posterior lateral eyes. First femur 1.8 mm, patella and tibia 2.0, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.7 mm, third 1.1, fourth 1.8. Femora shorter than corresponding patellae and tibiae, except third, which is slightly longer.

Male allotype. Coloration much darker than in female, with little white pigment. Dorsum of abdomen with a pair of white streaks anteriorly (Fig. 150), venter with two white spots. Total length 3.9 mm. Carapace 1.7 mm long, 1.3 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.5 mm, patella and tibia 1.7, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.4 mm, third 0.9, fourth 1.5. Length of femora shorter than adjacent patellae and tibiae, except third, which is of equal length.

Note. Males and females were collected together.

Diagnosis. The short body distinguishes this species from other *Cyclosa* without dorsal tubercles, as does the epigynum with its opening having round sides (Fig. 146) and a small posterior median plate (Fig. 147). The palpus has a narrow conductor tooth and a large barb on the median apophysis (arrow in Fig. 153).

Distribution. Known only from near Bogota, Colombia; no other specimens were found (Map 4D).

Cyclosa huila new species
Figures 154–161; Map 4D

Holotype. Female holotype from Finca Meremberg, 10 km E Santa Leticia [2°20′N, 76°13′W], 2,300 m elev., Depto. Huila, Colombia, Nov. 1979 (W. Eberhard, 1867a), in MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown (Fig. 156). Abdomen [poorly preserved in holotype] pear-shaped (Figs. 156, 157). Total length 5.0 mm. Carapace 1.5 mm long, 1.3 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.7 mm, patella and tibia 1.9, metatarsus 1.0, tarsus 0.6. Second patella and tibia 1.6 mm, third 1.0, fourth 1.7. Femora shorter than corresponding patellae and tibiae.

Male from Saladito. Coloration darker than that of female. Sternum dark brown. Abdomen dark with dorsal markings (Fig. 158), venter black with one pair of discrete white patches. Abdomen oval, with small posterior median tubercle (Fig. 158). Total length 2.7 mm. Carapace 1.63 mm long, 1.25 wide in thoracic region, 0.49 wide behind posterior lateral eyes. First femur 1.46 mm, patella and tibia 1.40, metatarsus 0.79, tarsus 0.46. Second patella and tibia 1.14 mm, third 0.65, fourth 1.30. Femora slightly longer than corresponding patellae and tibiae, except fourth, which is equal.

Note. Males and females were collected together at Saladito.

Variation. Total length of females 4.9 to 6.4 mm. The illustrations were made from female holotype and a male from Saladito.

Diagnosis. The female has a set off posterior extension on the abdomen (Fig. 157), and the epigynum depression in ventral view has two pairs of lips (Fig. 154) (Two pairs of lips can be seen in some other species in subventral view.) The male has a wide, parrot beak-shaped conductor (Fig. 159), and the median apophysis has a symmetrical lobe (Fig. 161).

Natural History. A vial contains a note with the comment that the species is social. The specimen from Dept. Nariño came from lowland rainforest.

Distribution. Southwestern Colombia (Map 4D).

Specimens Examined. COLOMBIA *Valle*: Saladito, km 18 on road from Cali to Buenaventura, 1975, 1♀; Sept. 1975, 1♀; Oct. 1975, 1♀, 2♂ (all W. Eberhard, MCZ). *Nariño*: Junin, West slope Andes, 340 m, 15 Dec. 1972, 3♀ (N. Leist, SMNK).

Cyclosa caroli (Hentz)
Figures 162–180; Map 5D

Epeira caroli Hentz, 1850: 24, pl. 3, fig. 15, ♀. Female type from Alabama destroyed.

Cyclosa lacerta O. P.-Cambridge, 1889: 50, pl. 7, fig. 14, ♂. Male lectotype designated by Levi (1977: 82) from Guatemala or Panama in BMNH, no. 1905.4.28.2846, examined. Keyserling, 1893: 275,

pl. 14, fig. 204, ♂. F. P.-Cambridge, 1904: 494, pl. 47, fig. 3, ♂. Synonymized by Levi (1977).

Cyclosa caroli:—Keyserling, 1893: 272, pl. 14, fig. 202, ♀. McCook, 1894: 277, pl. 17, figs. 7, 8, ♀, ♂. F. P.-Cambridge, 1904: 494, pl. 47, fig. 4, ♀. Roewer, 1942: 761. Bonnet, 1956: 1310. Levi 1977: 82, figs. 51–63, ♀, ♂.

Cyclosa elongata Franganillo, 1930: 68. Type specimen from Sierra Maestra and Montañas de Trinidad, Cuba, lost.

Description. Female from Chicanna Ruins, Mexico. Carapace dark brown, cephalic region darkest, lightest in posterior median region (Fig. 167). Abdomen venter dusky with black around spinnerets (Fig. 168). Abdomen with median posterior extension without tubercles (Figs. 167–169). Total length 6.0 mm. Carapace 1.74 mm long, 1.17 wide in thoracic region, 0.66 wide behind posterior lateral eyes. First femur 1.45 mm, patella and tibia 1.72, metatarsus 0.98, tarsus 0.52. Second patella and tibia 1.51 mm, third 0.87, fourth 1.52. Femora shorter than corresponding patellae and tibiae except third, which is of same length.

Male from Las Tuxtlas, Mexico. Carapace lighter than in female. Sternum dark brown. Abdomen darker than in female (Fig. 171), venter gray to black. Total length 3.1 mm. Carapace 1.50 mm long, 1.14 wide in thoracic region, 0.43 wide behind posterior lateral eyes. First femur 1.27 mm, patella and tibia 1.33, metatarsus 0.85, tarsus 0.42. Second patella and tibia 1.05 mm, third 0.63, fourth 1.20. Femora longer than corresponding patellae and tibiae, except fourth is the same length (male from Colombia).

Note. Males and females were collected together.

Variation. Total length of females 3.5 to 8.2 mm, most 5 and 7 mm; total length of males 2.5 to 4.2 mm, most between 2.5 and 3.5. Figures 162, 163, 172–176 were made from Mexican specimens; Figure 164 from a female from Colombia; Figure 165, 166, 177–180 from Bolivia; and Figure 170 from Peru.

Diagnosis. Unlike other species, *C. caroli* has the depressions hidden behind the base of a nearly round scape (Figs. 162, 164, 165); there are usually short, almost circular brows, and the posterior median plate is small (Figs. 163, 166). Females differ from *C. tapetifaciens* by having a slender abdomen (Figs. 167–169). The palpus of males has a wide conductor tooth (Figs. 173, 176, 177, 180) and a lobe and long distal tooth on the median apophysis (Fig. 172); it differs from similar species by having the conductor lobe projecting above the tooth in mesal view of the palpus (arrow in Fig. 173).

Natural History. Females have been collected at night in a coffee plantation in Puerto Rico; in rain forest in Chiapas, Mexico; in understory of rain forest at La Selva, Costa Rica; in wet forest and humid forest with cacao in Limon Prov., Costa Rica; by beating forest vegetation in Venezuela; from river vegetation in Magdalena, Colombia; in secondary oak forest in Boyaca, Colombia; and in high forest, Bolivia. Males have been collected in grassland edge of forest in Venezuela.

Distribution. Widespread from southeastern United States to Bolivia and São Paulo State, Brazil (Map 5D).

Specimens Examined. MEXICO *Baja California Sur*: 63 km S La Paz, road to Todas Santos, ♀ (CAS). *San Luis Potosí*: Huichihuayan, 21°19′N, 98°50′W ♀ (AMNH); 1.6 km W Tamazunchale, ♀ (AMNH); 8 km N Tamazunchale, ♀ (AMNH); Valles, ♀ (AMNH). *Veracruz*: Las Tuxtlas, 15 km N Catemaco, 50 m, 18°37′N, 95°07′W, ♀♂ (MCZ); Lago Catamaco, La Jungla 18°27′N, 95°05′W, ♀ (MCZ); La Buena Ventura, ♀ (AMNH); Fortín, ♀ (AMNH); Mirador Zacuapan, ♂ (AMNH); Potrero, ♀ (AMNH); 14.4 km SSW Veracruz, ♀ (AMNH). *Campeche*: Chicanna Ruins, 8 km W Xpujil, ♀ (W. Maddison, MCZ); 6 km W Francisco Escárcega, 18°37′N, 90°46′W, ♀ (MCZ). *Quintana Roo*: Kohunlich Ruins, 9 km S Francisco Villa, ♀ (W. Maddison, R. S. Anderson, MCZ). *Chiapas*: Selva del Ocote, 32 km W Ocozocautla, 762 m, ♀ (CAS); La Zacualpa, ♀ (AMNH); 9.6 km Finca Santa María, Huehuetan, ♂ (AMNH); Tapachula, ♀ (CAS). GUATEMALA Cobán, 1♂ (AMNH); Quirigua, ♀ (MCZ); Tikal, El Petén ♂ (CAS). COSTA RICA very common. PANAMA very common.

BAHAMA ISL. South Bimini, ♀ (AMNH). CUBA *Cienfuegos*: Soledad, ♂ (MCZ); Sierra da Trinidad, Mina Carlota, ♀ (MCZ). *La Havana*: La Havana, ♀ (MCZ); Río Ariguanabo, Antonio de los Baños, ♀ (MCZ); Cueva de Rincón de Guanabo, ♀ (AMNH).

Isla da Pines: Sierra las Casas, ♀ (AMNH). *Santa Clara*: Vega Alta, ♀ (AMNH). GRAND CAYMAN ISLAND ♀ (MCZ). JAMAICA *Westmoreland*: Negril, ♀ (MCZ). *St. Andrew Par*: Hope Gardens, ♀ (MCZ). DOMINICAN REPUBLIC Sabana de la Mar, ♀ (MCZ). PUERTO RICO Hacienda Juanita, Maricao, ♀ (MCZ); Mayagüez, ♀ (AMNH). LESSER ANTILLES *Eustatius*: The Quill, 280 m, ♀♂ (AMNH). *Grenada*: Grand Etang, ♀ (MCZ). *St. Vincent*: ♀ (MCZ). *Guadeloupe*: Basse Terre, 3–4 km W Moustique, ♀ (ANSP); nr. Goyarie W Moustique Island, ♀ (MCZ); Point-a-Pitre, ♀ (AMNH). *Montserrat*: Gage's Soufrière, ♀ (AMNH). TRINIDAD St. Augustine, ♂ (AMNH); St. Augustine River, ♀ (MCZ); St. Augustine Univ. Campus, ♀♂ (MCZ); *St. George*: Simla, Arima Valley, ♀ (AMNH).

VENEZUELA *Barinas*: main road betw. Barinas and Ciudad Bolivia, ♀ (USNM). *Guarica*: Guatapo Natl. Pk., Río Oritugo, ♂ (AMNH). *Bolívar*: 26 km N Yurnaní, Gn. Sabana, ♂ (AMNH). GUYANA Kartabo, ♀ (AMNH); Rupununi River nr. Mount Makarapan, ♀ (AMNH). COLOMBIA *Magdalena*: Pueblo Bello, Sierra Nevada de Santa Marta, ♂ (AMNH). *Boyacá*: Villa de Leiva, 2,480 m, 05°42′N, 73°29′W ♀ (MCZ). *Cundinamarca*: Finca Bella Vista nr. Sasaima, ♂ (CAS). *Meta*: Carimagua, ♀♂ (MCZ); Lomalinda nr. Puerto Lleras, ♀♂ (MCZ, CAS); 15 km SW Puerto Lopez, ♀♂ (MCZ); 6 km SW Puerto Lopez, ♀♂ (MCZ). *Antioquia*: Guarne, 2,000 m, ♂ (MCZ); San Vicente, ♀ (MCZ). *Córdoba*: Ayapel nr. Cienaga, ♀♂ (MCZ). *Valle*: Anchicayá, ♀ (MCZ); 50 km S Buenaventura (MCZ); Lago Calima, betw. Buga & Loboquerrero, ♀ (MCZ); 21 km W Cali, ♀♂ (CAS); Río San Juan, afl. del Digua, nr. Queremal, ♀ (MCZ); above Saladito, 1,800 m, ♀♂ (MCZ); nr. Saladito, 1,600 m, ♀♂ (MCZ). *Cauca*: 90 km S Cali, ♀♂; betw. Prendama & Monodomo, ♀ (MCZ); N of Prendamo, ♀ (MCZ); 10 km N Piendano, ♀♂ (MCZ). *Nariño*: La Planada, 7 km S Chocones, 1,800 m, ♀♂ (MCZ); La Espriella, 50 m, ♀ (CV). Chachaquil nr. airport, ♀ (SMNK). ECUADOR *Sucumbíos*: Cuyabeno, bridge over Cuyabeno, betw. Tarapoa and Tipishca, ♀ (MCZ); Reserva Faunistica Cuyabeno, Laguna Grande, 2–5 Aug. 1988, ♀ (MCZ). *Imbabura*: Los Cedros, Biological Sta., 00°18′S, 78°46′W, ♀ (MCZ). *Pichincha*: Río Flor Palmeras, ♀ (MECN); 4 km NE Pedro Vicente Madonado, km 113 on road Quito to Puerto Quito, ♂ (MCZ); Tinalandia nr. Santo Domingo de las Colorados, ♀ (CAS). *Manabi*: Manta, ♀♂ (CAS). *Chimborazo*: Amula, ♀ (MNHN 10498). *Guayas*: Guayaquil, ♀♂ (CAS). *El Oro*: Buenavista, 20 km SE Machala, ♀♂ (CAS). PERU *Loreto*: Jenaro Herrera, ♀ (MUSM). *Piura*: Quebrada Pariñas, ♀♂ (CAS); Quebrada Sangora, ♀ (CAS); Quebrada Mogollon, ♀♂ (CAS); El Muerto, ♀♂ (CAS). *Pasco*: Oxapampa, ♀ (MUSM). *Madre de Dios*: Zona Reservada Pakitza, ♀ (MUSM, USNM). *Cuzco*: Wiñayhuaina, 13°07′S, 72°34′W, 2,700–3,100 m, ♀ (MUSM). BRAZIL *Roraima*: Ilha de Maracá, Rio Uraricoera, ♀ (MCN 27082, 27083); ♀ (INPA); Ularacá, ♀ (INPA). *Amazonas*: Reserva Ducke, 80 km N Manaus, ♀ (MCN 27086). *Pernambuco*: Dois Irmãos, ♀ (MCN 25792). *Mato Grosso*: Chavantina, ♀ (MZSP 1324, 1325, 4541). *Espírito Santo*: Reserva Florestal de Linhares, ♀ (MCZ). *São Paulo*: Campos do Jordão, ♀ (MZSP 1318). BOLIVIA *Beni*: Estacion Biologica, ♀ (USNM). *La Paz*: Sainani, Vale de Zongo, ♀♂ (MCN).

Cyclosa tapetifaciens Hingston
Figures 181–194; Map 5A

Cyclosa tapetifaciens Hingston, 1932: 80, 370. Female holotype from Essequibo River, Guyana, in BMNH, lost. Female neotype, here designated, from Santarém, Alter de Chão, Est. Pará, Brazil, 26 Jan. 1994 (H. Höfer), in MCN 25284. The neotype was collected with another female and a male. Roewer, 1942: 760. Bonnet, 1956: 1324.

?*Cyclosa tremula* Hingston, 1932: 95, 370. Male (?) from Essequibo River, Guyana, lost. Roewer, 1942: 760. Bonnet, 1956: 1324. NEW SYNONYMY.

Cyclosa filiobliqua Hingston, 1932: 108, 121, 371. Immature from Essequibo River, Guyana, lost. Roewer, 1942: 759. Bonnet, 1956: 1316. NEW SYNONYMY.

Parazygia accentonotata di Caporiacco, 1955: 345, fig. 30, ♂. Male holotype from Rancho Grande, Aragua, Venezuela, in MBCV, Caracas, examined. NEW SYNONYMY.

Cyclosa sumaqkay Archer, 1971: 150, fig. 7, ♀. Female holotype from Tingo María, Depto. Húanuco, Peru, in AMNH, examined. Brignoli, 1983: 266. NEW SYNONYMY.

Note. The diagnostic features described

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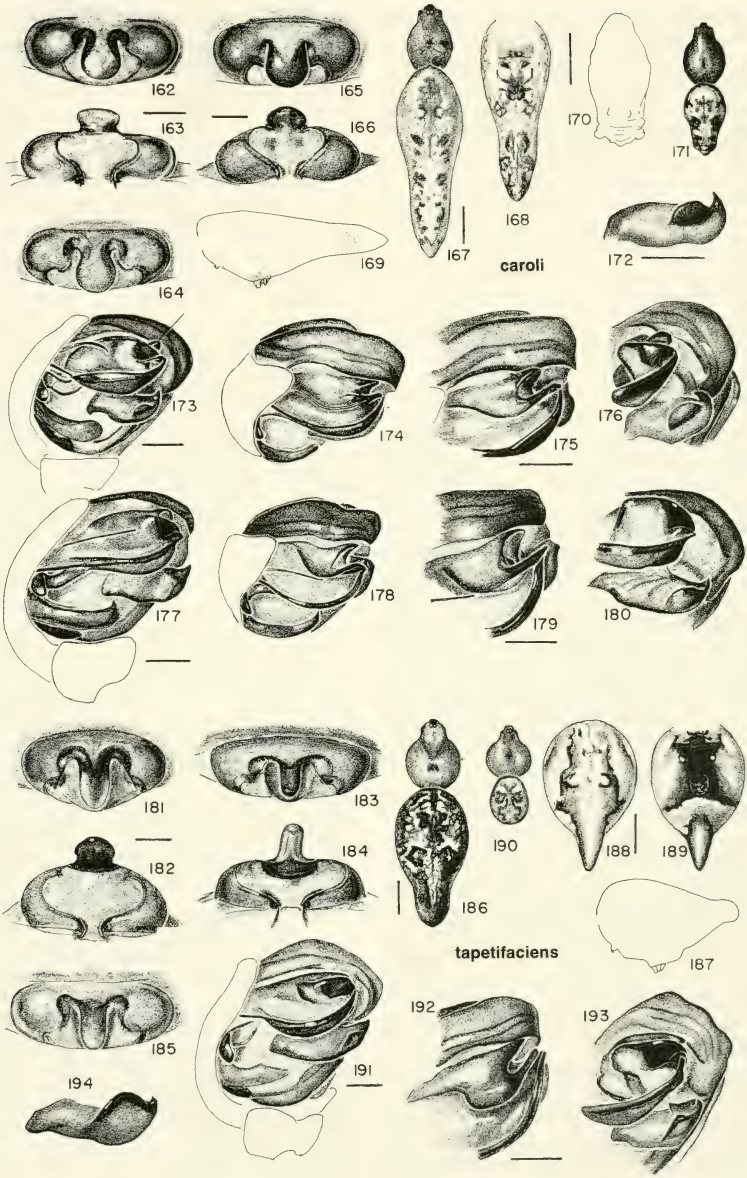
Figures 162–180. *Cyclosa caroli* (Hentz). 162–170, female. 162–166, epigynum. 162, 164, 165, ventral. 163, 166, posterior. 162, 163, (Mexico). 164, (Depto. Nariño, Colombia). 165, 166, (Beni Prov., Bolivia). 167, dorsal. 168, abdomen, ventral. 169, abdomen, lateral. 170, shrivelled abdomen (Depto. Piura, Peru). 171–180, male. 171, dorsal. 172–180, left palpus. 172, 176, 180, median apophysis. 173, 177, mesal. 174, 175, 178, 179, apical. 172–176, (Veracruz, Mexico). 177–180, (La Paz, Bolivia).

Figures 181–194. *C. tapetifaciens* (Hingston). 181–189, female. 181–185, epigynum. 181, 183, 185, ventral. 182, 184, posterior. 181, 182, (Santarém, Brazil). 183, 184, (Ecuador). 185, (Depto. Huánuco, Peru). 186, Dorsal. 187, abdomen, lateral. 188, abdomen, dorsal. 189, abdomen, ventral. 188, 189, (Mt. Neblina area, Venezuela). 190–194, male. 190, dorsal. 191–194, palpus. 191, mesal. 192, apical. 193, 194, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.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by Hingston for *C. tapetifaciens* are the oval abdomen, less elongated than in *C. caroli,* which this species resembles; lacking shoulder humps, and having the posterior end pointed, without tubercles. Total length 4 mm. A specimen collected by Hassler from Guyana (AMNH) was determined by Caporiacco as *C. tapetifaciens* (as were specimens of some different species).

Cyclosa tremula (2 mm in total length) and *C. filiobliqua,* (1.75 mm long) both have the abdomen oval, not elongated, no shoulder humps, and posterior pointed with no protuberances. Both are probably *C. tapetifaciens.*

Description. Female from Sauri-Wau River, Guyana. Carapace yellow, thoracic region brown (Fig. 186). Abdomen venter contrasting white and black. Abdomen without dorsal tubercles (Figs. 186, 187). Total length 5.4 mm. Carapace 1.9 mm long, 1.3 wide in thoracic region, 0.8 wide behind posterior lateral eyes. First femur 1.9 mm, patella and tibia 2.3, metatarsus 1.4, tarsus 0.6. Second patella and tibia 1.9 mm, third 1.1, fourth 1.9. All femora shorter than corresponding patella and tibia.

Male from Santarém, Brazil. Carapace brown with a pair of lighter areas, side by side in middle of thorax (Fig. 190). Abdomen with usual pattern (Fig. 190), venter black with a pair of white spots. Total length 3.2 mm. Carapace 1.69 mm long, 1.37 wide in thoracic region, 0.48 wide behind posterior lateral eyes. First femur 1.65 mm, patella and tibia 1.72, metatarsus 1.04, tarsus 0.52. Second patella and tibia 1.27 mm, third 0.78, fourth 1.53. First femora shorter than corresponding patellae and tibiae, second same length, third and fourth longer.

Note. Males and females have been collected together.

Variation. Total length of females 4.4 to 7.7 mm, males 2.7 to 3.7. Some Peruvian specimens have an all-white sternum. One specimen from near Mt. Neblina, Venezuela, had a contrasting pattern, unlike all others (Figs. 188, 189). The male illustrated came from Santarém, Brazil.

Diagnosis. The scape of the epigynum is wide and the diameter of the depression on each side small, less than the diameter of the scape, the brow slightly wider than the scape (Figs. 181, 183, 185). The posterior median plate (Figs. 182, 184) is wider than that of *C. caroli* (Fig. 163). The palpus differs from others in that the notch of the conductor has parallel sides (Fig. 192) and the tooth of the median apophysis is shorter than the height of the lobe (Fig. 194), whereas the tooth of the median apophysis of *C. caroli* is equal to the height of the lobe (Fig. 172).

Natural History. Specimens were collected in moist tropical forest in Depto. Meta, Colombia; in secondary rain forest in Depto. Nariño, Colombia, from low foliage in Neblina Mountain vicinity; in forests near Belém; in campo grassland and dry forest north of Xavantina, Brazil; by canopy fogging at Tambopata, Peru; and has been found as prey of sphecid wasps north of Manaus.

Distribution. Widespread from Panama to Rio Grande do Sul, Brazil, and Misiones Prov., Argentina (Map 5A).

Specimens Examined. PANAMA *Chiriquí*: Bugaba, ♀ (MIUP); Cerra Cementerio, Bugaba, Río Mula, ♀ (MIUP); Panama City, ♀ (CAS). VENEZUELA *Monagas*: Caripe, outside Cueva del Guacharo, 1,065 m, ♀ (USNM). *Miranda*: 35 km N Altagracia, Guatopo Natl. Park, Agla Blanco, 400 m, ♀ (AMNH). *Aragua*: Henri Pittier Natl. Park, Rancho Grande, 1,500 m, ♀♂ (USNM); Rancho Grande, ♀ (AMNH); ♀♂ (AMNH); ♀ (AMNH). *Mérida*: La Carbora, NW Merida, road to Azuleta, 2,200 m, ♀ (MCZ). *Amazonas*: Cerro de la Neblina, 0°50′N, 66°10′W, ♀ (USNM). GUYANA Sauri-Wau River nr. Tacutu River, ♀ (AMNH); Tumatumari, ♀ (AMNH). SURINAM *Brokopondo*: Brownsberg, 4°50′N, 55°15′W, ♀ (MCZ). COLOMBIA *Meta*: Carimagua, ♀ (MCZ); Macarena, 450 m, Río Duda, 2°40′N, 74°10′W, ♀ (MCZ); Hacienda Mozambique, 15 km SW Puerto Lopez, ♀♂ (MCZ). *Antiochia*: San Vicente, ♀ (MCZ). *Valle*: Atuncela, ♀♂ (MCZ); nr. Cali, ♀ (MCZ); ♂ (MCZ); ♂ (MCZ); ♂ (MCZ); above Habana, 2,200 m [dead end road E Palmira], ♀ (MCZ); Río Jamundi nr. Cali, 1,000 m, ♀ (MCZ); ♀ (MCZ); Río Jamundi betw. Cali and Jamundi, ♀ (MCZ); ♀ (MCZ); Cent. Hid. Anchicava, 400 m, ♂ (MCZ). *Amazonas*: Araracuara, ♀ (CV). *Nariño*: El Diviso,

560 m, ♀ (CV). ECUADOR *Sucumbíos*: Reserva Forestal Cuyabeno, ♀ (MCZ); Cuyabeno Tarapoa, 0°07′S, 76°20′W, ♀ (MCZ); Cuyabeno bridge, road betw. Tarapoa and Tipishca, 0°01′S, 76°18′W, ♀ (MCZ). *Napo*: Pompeya, ♀ (MCZ). *Pichincha*: km 113 via Puerto Quito, ♀ (MCZ); ♀ (MECN); ♀♂ (MCZ); Pululahud, ♀ (RSNB); Tinalandia, 12 km E Santo Domingo Colorados, ♀♂ (FSCA). *Bolívar*: Balzapampa, ♂ (AMNH). *Manabi*: above Pedernales, 0°02′N, 80°00′W, ♀ (MECN). *Guayas*: Colonche, ♀ (CAS); W Guayaquil, ♂ (CAS); 16 km N Manglaralto, ♀ (E. I. Schlinger, E. S. Ross, CAS); Milagro, ♀ (CAS). PERU *Loreto*: Explorama Lodge, 80 km NE Iquitos, ♀ (FSCA); Pebas (and São Paulo Olivença, Amazonas, Brazil), ♀ (MNHN 4095c); Río Samiria, 04°43′S, 74°18′W, ♀♂ (MUSM); Cocha Shinguito, 05°08′S, 74°45′W, ♀ (MUSM). *Piura*: Higuerón, Las Lomas, ♀♂ (CAS). *Ucayali*: Bosque Nacional A. von Humboldt, ♀ (MUSM). *Huánuco*: Cueva de las Lechuzas, ♀ (AMNH); 8 km W Las Palmas, ♀ (CAS); Panguana, 09°37′S, 74°56′W, ♀ (MCZ); Santa Teresa, Río Huallaga, 600 m, ♀ (CAS). *Pasco*: Oxapampa, ♀ (MUSM); 2 km La Suiza, Chantabamba, ♀ (MUSM). *Madre de Dios*: Zona Reservada Pakitza, 11°56′S, 71°17′W, ♀ (MUSM); ♀ (USNM); Zona Reservada Tambopata, Explorer's Inn, ♀ (MCZ); ♂ (USNM); ♀ (MCZ); ♀ (MUSM); ♀ (USNM). BRAZIL *Pará*: Belém, ♀ (MCZ); Fazenda Velha, Belém, ♀ (MACN). *Roraima*: Maraca Island, Rio Uraricoera, ♀ (MCN 27087). *Amazonas*: Río Autas, Cururuzinho, ♀ (NRMS); Manaus, ♂ (MACN); Smithsonian areas 80 km N Manaus, ♀♂ (SMNK); 80 km N Manaus, ♀ (MCZ); Colosso Reserve, 80 km N Manaus, ♀♂ (MCZ); Km 41 Reserve, 80 km N Manaus, ♀ (MCZ); Reserva C. de Powell, 80 km N Manaus, ♀ (MCZ); Manaus, Reserva Ducke, ♀ (MCN 27084); ♀ (MCN 23938); ♀ (MCN 22079); Curari Isl., Manaus, ♀ (MCN 27085); Ulanzus, ♀ (INPA); Estação Ecológica de Mamiravá, Tefé, ♀ (MCN 22930, 23112); Manés, ♀ (MCN 27081). *Goiás*: Rio Araguaia, Araguças, ♀ (MZSP 1213). *Rondônia*: Abuná, ♀ (MCZ). *Bahia*: Encruzilhada, 900 m, ♀♂ (AMNH); Fazenda Almada, Uruçuca, ♀ (MCN 10491); Fazenda São Roque, Camacan, ♀ (MCN 11043); Fazenda Matiapa, Camacan, ♀ (MCN 1193). *Espírito Santo*: Reserva Florestal de Linhares, ♀ (MCZ). *Mato Grosso*: Chapada da Guimarães, ♀ (MCP 2168); Chavantina, ♀ (MZSP 4541a); 260 km N Xavantina, 12°49′S, 51°46′W, ♀ (MCZ). *Mato Grosso do Sul*: Urubupungá Falls on Rio Paraná, 20°36′S, 51°33′W, ♀ (MZSP 13153). *Paraná*: Parque Nacional do Iguaçu, Foz do Iguaçu, ♀ (MCN 23499); ♀ (MCZ); ♀ (SMNK); Rio Negro, ♂ (MNRJ 58262); Salto Caxias Rio Iguaçú, Capitão Leonidas, ♀ (MCN 23297). *Santa Catarina*: Nova Teutonia, ♂ (SMF). *Rio Grande do Sul*: Montenegro, ♀ (MCN 6807); São Leopoldo, ♀ (MCP 0346). PARAGUAY *Alto Paraná*: Taquarazapa, ♀ (AMNH). BOLIVIA Mamuré Geb. [Gebiet, Gebirge, ?, area, mountains], nothern Bolivia, ♀♂ (SMF). *Beni*: Estacion Biol. Beni, 14°47′S, 66°15′W, ♀ (USNM). *La Paz*: Cerro Uchumachi, 7 km SW Coroico, 16°15′S, 67°21′W, 1,900 m, ♀ (USNM). *Cochabamba*: Yungas Chaparé, ♀ (AMNH); Espíritu Santo, ♀ (MNHN 15716). ARGENTINA *Misiones*: Montecarlo, ♂ (MACN); Parque Nacional Iguazú, ♂ (MACN); Puerto Bemberg [Puerto Libertad], ♀ (MACN 3135); ♀ (MACN 2997); ♀ (MACN 3417); Puerto 17 Octubre [Puerto Libertad], ♀ (MACN 3889); Santa Ana, ♀ (MACN); Santa María, ♀ (MACN); ♀ (MACN 3891).

Cyclosa donking new species
Figures 195–198; Map 5B

Holotype. Female holotype from Estacion Biológica Beni, 14°47′S, 66°15′W, Depto. Beni, Bolivia, ca. 225 m, 8–14 Nov. 1989 (J. Coddington, S. Larcher, A. Penaranda, C. Griswold, D. Silva), in USNM. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace yellow (Fig. 197). Coxae and distal leg articles yellow without rings. Abdomen dorsally white with dense white pigment spots (Fig. 197); venter with dense white pigment spots between epigynum and spinnerets, less dense in surrounding area. Abdomen elongate drop-shaped (Figs. 197, 198). Total length 7.0 mm. Carapace 2.0 mm long, 1.5 wide in thoracic region, 0.8 wide behind posterior lateral eyes. First femur 2.0 mm, patella and tibia 2.3, metatarsus 1.2, tarsus 0.6. Second patella and tibia 2.0 mm, third 1.2, fourth 1.9. Length of femora shorter than corresponding patellae and tibiae.

Diagnosis. This species is distinguished by the shape of the abdomen (Figs. 197, 198), the lack of black pigment and rings on legs, and by the shape of the epigynum, which is similar to that of *C. caroli* (Figs. 162, 163). The scape is not constricted at its base and the brows and depression are more posterior (Figs. 195, 196) than in *C. caroli*.

Distribution. Known only from type locality in Bolivia (Map 5B); no other specimens were collected.

Cyclosa oseret new species
Figures 199–203; Map 3C

Holotype. Female holotype from Teresópolis, 900 to 1,000 m, Est. Rio de Janeiro, Brazil, March 1946

(H. Sick), in AMNH. The specific name is an arbitrary combination of letters.

Description. Female holotype. Carapace yellow-white with a median tiny brown spot (Fig. 201). Sternum brown with an anterior transverse white line and posteriorly, a short, longitudinal white line. Abdomen white with a pair of indistinct spots in middle (Fig. 201); venter with black and white patches (Fig. 202). Abdomen with a pair of ventral tubercles and a median posterior extension (Fig. 203). Total length 4.1 mm. Carapace 1.53 mm long, 1.04 wide in thoracic region, 0.62 wide behind posterior lateral eyes. First femur 1.30 mm, patella and tibia 1.53, metatarsus 0.86, tarsus 0.47. Second patella and tibia 1.30 mm, third 0.79, fourth 1.30. All femora shorter than corresponding patellae and tibiae.

Diagnosis. *Cyclosa oseret* differs from others by having a round, stalked scape with a round depression on each side (Fig. 199).

Distribution. Known only from the type locality (Map 3C).

Cyclosa turvo new species
Figures 204–207; Map 3C

Holotype. Female holotype, from Parque do Turvo, Tenente Portela, Rio Grande do Sul, Brazil, 4–6 Feb. 1980 (A. A. Lise), in MCN no. 8969 A. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown (Fig. 206). Sternum light brown with dark border. Abdomen venter black with U-shaped remnants of white patches. Abdomen with a posterior extension (Figs. 206, 207). Total length 4.7 mm. Carapace 1.2 mm long, 0.8 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.0 mm, patella and tibia 1.3, metatarsus 0.7, tarsus 0.4. Second patella and tibia 1.2 mm, third 0.6, fourth 1.1. Femora shorter than patella and tibia of same leg.

Diagnosis. *Cyclosa turvo* differs from *C. oseret* (Fig. 199) and *C. caroli* (Fig. 162) in that the scape of the epigynum lacks a constriction at its anterior end (Fig. 204) and in having a large posterior median plate (Fig. 205).

Distribution. Known only from the type (Map 3C); no other specimens were found.

Cyclosa mavaca new species
Figures 208–211; Map 3B

Holotype. Female holotype and immature paratype from Alto Mavaca base camp, upper Río Mavaca, 228 m, 02°01′30″N, 65°07′00″W, Amazonas State, Venezuela, 31 Jan. 1989 (D. A. Polhemus), in USNM. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown, lightest in eye region (Fig. 210). Sternum dark brown with anterior transverse white band and posterior, median white spot. Abdomen venter black between epigynum and spinnerets with an inverted white "T", the median white areas indistinct. Abdomen almost cylindrical (Figs. 210, 211). Total length 5.0 mm. Carapace 1.4 mm long, 0.9 wide in thoracic region, 0.5 wide behind posterior lateral eyes. First femur 1.1 mm, patella and tibia 1.4 , metatarsus 0.7, tarsus 0.4. Second patella and tibia 1.1 mm, third 0.7, fourth 1.1. Femora shorter than corresponding patellae and tibiae, except third is of same length.

Variation. Total length of females 4.2 to 5.1 mm.

Diagnosis. This species is distinguished by the wide scape of the epigynum, wider than the lateral areas of the base (Fig. 208); the scape hides the openings. It differs from others with a round scape, except *C. turvo*, by the relatively wide posterior median plate (Fig. 209).

Natural History. Specimens came from vegetation.

Distribution. Known only from southern Venezuela and southeastern Colombia (Map 3B).

Specimens Examined. COLOMBIA *Amazonas*: Araracuara, 270 m, 23 Feb. 1988, 2♀ (C. Valderrama, CV, MCZ).

Cyclosa camargoi new species
Figures 212–217; Map 3C

Holotype. Female holotype from Campos do Jordão, São Paulo State, Brazil, 3 Jan. 1948 (F. Lane), in MZSP no. 1318. The species is named after the arachnologist H. F. de Almeida Camargo, who recognized that the specimen belonged to a new species.

Note. The specimen had been labeled *Cyclosa jordanensis* Camargo and Soares, holotype. Apparently it is a manuscript type and was never published.

Description. Female holotype. Carapace dark brown, eye region light yellowish (Fig. 216). Sternum light yellowish. Abdomen venter whitish with gray patches. Abdomen almost cylindrical, posterior almost as wide as anterior (Figs. 216, 217). Total length 7.0 mm. Carapace 2.0 mm long, 1.2 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.6 mm, patella and tibia 2.0, metatarsus 1.0, tarsus 0.6. Second patella and tibia 1.7 mm, third 1.0, fourth 1.6. Femora shorter than corresponding patellae and tibiae.

Variation. Total length of females 4.8 to 7.0 mm. Figures 212, 213, 216, 217 were made from the holotype.

Diagnosis. This species, like *C. caroli* (Fig. 162), has a wide, sometimes almost circular scape, but the median plate is wider both anteriorly and posteriorly (Figs. 212–215). The sculpturing of the base is difficult to see. The shape of the abdomen (Figs. 216, 217) is unlike that of any other American *Cyclosa* species.

Distribution. Southern Brazil (Map 3C).

Specimens Examined. BRAZIL *Rio de Janeiro*: Ilha Grande, sea level, 15 Mar. 1944, 1♀ (H. Sick, AMNH); Teresópolis, 1,000 m, 9 Mar. 1946, 1♀ (H. Sick, AMNH). *São Paulo*: Cocaia, Represa Nova, Santo Amaro, 4 Apr. 1948, 1♀ (H. Urban, MZSP 13160); Ilha São Sebastião, 16–19 Jan. 1950, 1♀ (H. Urban, MZSP 7696). *Rio Grande do Sul*: Esteio, 3 Aug. 1958, 1♀ (J. A. Petersen, MCP 3878).

Cyclosa teresa new species
Figures 218–222; Map 5B

Holotype. Male holotype from Santa Teresa, Est. Espírito Santo, Brazil, 5 Oct. 1942 (B. Soares), in MZSP no. 13150. The specific name is a noun in apposition after the locality.

Description. Male holotype. Carapace yellow and orange (Fig. 218). Chelicerae yellow. Labium, endites orange. Sternum orange with anterior transverse yellowish band. Coxae orange, first two femora orange; otherwise, legs yellow with orange rings. Dorsum of abdomen colorless with gray folium posteriorly, indistinct white patches anteriorly (Fig. 218), sides gray; venter gray with a pair of white spots. Total length 2.8 mm. Carapace 1.56 mm long, 1.23 wide in thoracic region, 0.48 wide behind posterior lateral eyes. First femur 1.56 mm, patella and tibia 1.53, metatarsus 0.96, tarsus 0.52. Second patella and tibia 1.23 mm, third 0.65, fourth 1.25. All femora slightly longer than corresponding patellae and tibiae.

Variation. Total length of males 2.8 to 3.0 mm. The illustrations were made from the holotype.

Diagnosis. Unlike other species, *C. teresa* has the notch of the conductor pointed in apical view (Fig. 220) and the tooth of the median apophysis behind the lobe (Figs. 221, 222). One male had ventral tubercles on the abdomen.

Distribution. Southeastern Brazil (Map 5B).

Specimens examined. BRAZIL *Santa Catarina*: Concordia, 27°08′S, 51°54′W, 30 Jan. 1996, 1♂ (A. B. Bonaldo, MCN 27267).

Cyclosa dianasilvae new species
Figures 223–231; Map 5C

Holotype. Female holotype, male allotype, 16 female, four male and nine immature paratypes from Zona Reservada Tambopata, 290 m, 12°50′S, 69°17′W, Madre de Dios, Peru, 13 May 1988 (D. Silva), in MUSM, one pair in MCZ. The species is named after the collector and arachnologist Diana Silva.

Description. Female holotype. Carapace dark brown, eye region lighter (Fig. 225). Sternum dark brown without marks. Abdomen venter black with tiny white patches (Fig. 226). Abdomen with a median posterior extension and without dorsal tubercles (Figs. 225–227). Total length 4.3

mm. Carapace 1.5 mm long, 0.8 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.2 mm, patella and tibia 1.6, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.4 mm, third 0.8, fourth 1.3. Femora shorter than corresponding patellae and tibiae, except third is of equal length.

Male allotype. Coloration darker than in female. Sternum dark brown, unmarked. Legs yellow, not ringed. Abdomen venter black without white or paired white spots. Abdomen oval (Fig. 228). Total length 2.6 mm. Carapace 1.39 mm long, 0.97 wide in thoracic region, 0.41 wide behind posterior lateral eyes. First femur 1.07 mm, patella and tibia 1.17, metatarsus 0.74, tarsus 0.42. Second patella and tibia 1.00 mm, third 0.61, fourth 1.01. Femora shorter than corresponding patellae and tibiae, except third, which is slightly longer.

Note. Males and females were collected together.

Variation. Total length of females 3.8 to 6.0 mm, males 2.6 to 2.8 mm. The illustrations were made from the female holotype and male allotype.

Diagnosis. Unlike most species, *C. dianasilvae* has the sternum dark brown without marks. The epigynum differs from others by having the lateral plates in ventral view narrower than the median plate to the side of the scape (Fig. 223). The male has a distinct, wide notch on the conductor in apical view (Fig. 230), and the lobe of the median apophysis is pointed and without distal tooth (Fig. 231).

Distribution. Ecuador, Peru, Amazon area (Map 5C).

Specimens Examined. ECUADOR *Sucumbíos*: Reserva Forestal Cuyabena, 23 July 1986, 1♀ (L. Avilés, MCZ). *Pastaza*: Puyo, 18 Apr. 1958, 1♂ (R. W. Hodges, MCZ). PERU *Loreto*: Jenaro Herrera, 04°45'S, 73°45'W, 26–28 Aug. 1988, 8♀, 1♂ (D. Silva, MUSM). *Madre de Dios*: Zona Reservada Tambopata, 5 June 1988, 2♀ (D. Silva, MUSM); Zona Reservada Tambopata, Bosque Alto, 31 July 1987, 5♀ (D. Silva, MUSM).

Cyclosa cajamarca new species
Figures 232–235; Map 5C

Holotype. Female holotype, six female paratypes from Llama, 2,300 m, west slope of Andes, between Chiclayo and Cutervo, Depto. Cajamarca, Peru, 10 June 1956 (W. Weyrauch), in CAS, one paratype in MCZ. The specific name is a noun in apposition after the locality.

Note. The specimens are in poor condition and may once have been dry.

Description. Female holotype. Carapace brown, cephalic region yellowish (Fig. 234). Abdomen white with folium posteriorly (Fig. 234); venter black with five white patches, the median largest. Abdomen with a pair of dorsal tubercles and a median posterior extension (Figs. 234, 235). Total length 6.2 mm. Carapace 1.5 mm long, 1.1 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.4 mm, patella and tibia 1.9, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.6 mm, third 0.9, fourth 1.4. Femora shorter than corresponding patellae and tibiae, except third, which is the same length.

Diagnosis. Cyclosa cajamarca is distinguished by having the openings of the epigynum with a straight lip, parallel to the median axis of the spider (Fig. 232) and the posterior median plate relatively small (Fig. 233).

Distribution. Known only from type locality in Peru (Map 5C); no other specimens were found.

Cyclosa libertad new species
Figures 236–239; Map 4E

Holotype. Female holotype and one immature from between Chagnal (07°50'S, 77°38'W) and Patos

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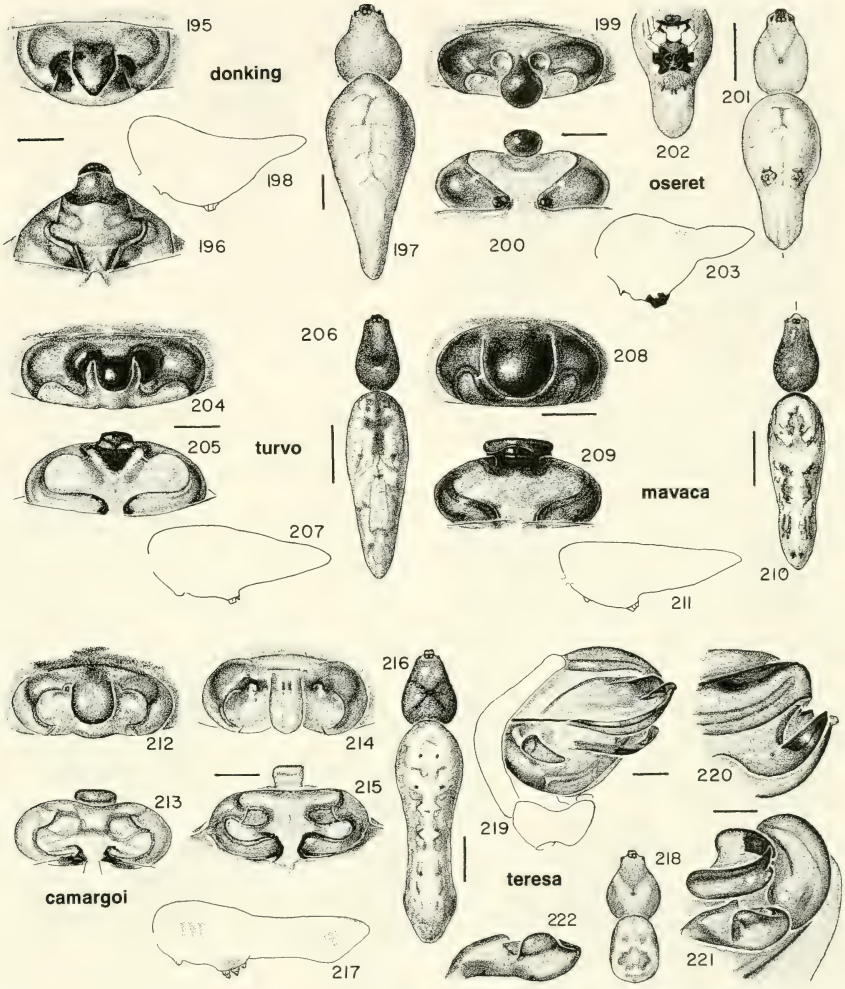
Figures 195–198. *Cyclosa donking* n. sp., female. 195, 196, epigynum. 195, ventral. 196, posterior. 197, dorsal. 198, abdomen, lateral.

Figures 199–203. *C. oseret* n. sp., female. 199, 200, epigynum. 199, ventral. 200, posterior. 201, dorsal. 202, abdomen, ventral. 203, abdomen, lateral.



Figures 204–207. *C. turvo* n. sp., female. 204, 205, epigynum. 204, ventral. 205, posterior. 206, dorsal. 207, abdomen, lateral.

Figures 208–211. *C. mavaca* n. sp., female. 208, 209, epigynum. 208, ventral. 209, posterior. 210, dorsal. 211, abdomen, lateral.

Figures 212–217. *C. camargoi* n. sp., female. 212–215, epigynum. 212, 214, ventral. 213, 215, posterior. 212, 213, (São Paulo, Brazil). 214, 215, (Rio Grande do Sul). 216, dorsal. 217, abdomen, lateral.

Figures 218–222. *C. teresa* n. sp., male. 218, dorsal. 219–222, left palpus. 219, mesal. 220, apical. 221, 222, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

(10°45'S, 71°45'W), 1,000 to 2,000 m, Depto. La Libertad, Peru, 27 Mar. 1988 (D. Silva D.), in MUSM. The specific name is a noun in apposition after the locality, La Libertad.

Description. Female holotype. Carapace brown, lighter between median and lateral eyes (Fig. 238). Abdomen venter black with a pair of distinct white patches and between them and slightly anterior, a median white patch. Abdomen with a pair of small dorsal tubercles and a median posterior extension (Figs. 238, 239). Total length 5.4 mm. Carapace 1.7 mm long, 1.2 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.5 mm, patella and tibia 1.7, metatarsus 0.9, tarsus 0.4. Second patella and tibia 1.5 mm, third 0.9, fourth 1.5. Femora shorter than corresponding patellae and tibiae, except third, which is of equal length.

Variation. Total length of females 5.3 to 6.8 mm. The specimen from Paute has the dorsal tubercles indistinct; the one from Baños lacks tubercles and has a narrower abdomen.

Diagnosis. *Cyclosa libertad* is distinguished by having an anterior, dorsal pair of tubercles on the abdomen (Figs. 238, 239), whereas *C. tapetifaciens* lacks these tubercles (Figs. 186, 187); also in *C. libertad* the scape of the epigynum (Fig. 236) is narrower than that of *C. tapetifaciens* (Fig. 181).

Distribution. Ecuador and northeastern Peru (Map 4E).

Specimens Examined. ECUADOR *Tungurahua*: Baños, 1,900 m, Oct 1938, 1♀ (W. Clarke-Macintyre, AMNH). *Azuay*: 17.6 km E Paute, 17 Feb. 1955, 1♀ (E. I Schlinger, E. S. Ross, CAS). PERU *La Libertad*: Pataz, 2,800 m, 16 June 1986, 1♀ (B. Roth, CAS). *Ancash*: Chiquían, Río Pativilca, 3,450 m, 7 Mar. 1956, 2♀ (F. Weyrauch, CAS).

Cyclosa curiraba new species
Figures 240–243; Map 5C

Holotype. Female holotype from Estacion Biológica Beni, trail south of camp in area of Río Curiraba and toward savanna, Dpto. Beni, Bolivia, 6 Sept. 1987 (S. Larcher, J. Coddington, J. P. Arce), in USNM. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace yellow with brown frame around thoracic region. Abdomen venter between epigynum and spinnerets black containing a pair of large white patches and scattered small white spots. Abdomen pear-shaped (Figs. 242, 243). Total length 5.4 mm. Carapace 1.7 mm long, 1.3 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.7 mm, patella and tibia 1.9, metatarsus 1.1, tarsus 0.5. Second patella and tibia 1.6 mm, third 1.0, fourth 1.7. Femora shorter than corresponding patellae and tibiae.

Variation. Total length of females 4.6 to 5.4 mm. In the female from Yucomo, the scape is wider than in other specimens. The illustrations were made from the holotype and another specimen.

Diagnosis. This species is distinguished from other *Cyclosa* species with a pear-shaped abdomen by the V-shaped brows of the epigynum (Fig. 240) and the triangular posterior median plate (Fig. 241).

Distribution. Bolivia (Map 5C).

Specimens Examined. BOLIVIA *Beni*: 27 km SW Yucomo, 15°23'S, 66°59'W, 15–19 Nov. 1989, 1♀ (J. Coddington et al., USNM); Estacion Biológica Beni, 5 km N Est. El Porvenir, 14 Sept. 1987, 3♀ (J. Coddington et al., USNM, MCZ); Estacion Biológica Beni, 8–14 Nov. 1989, 2♀ (J. Coddington et al., USNM).

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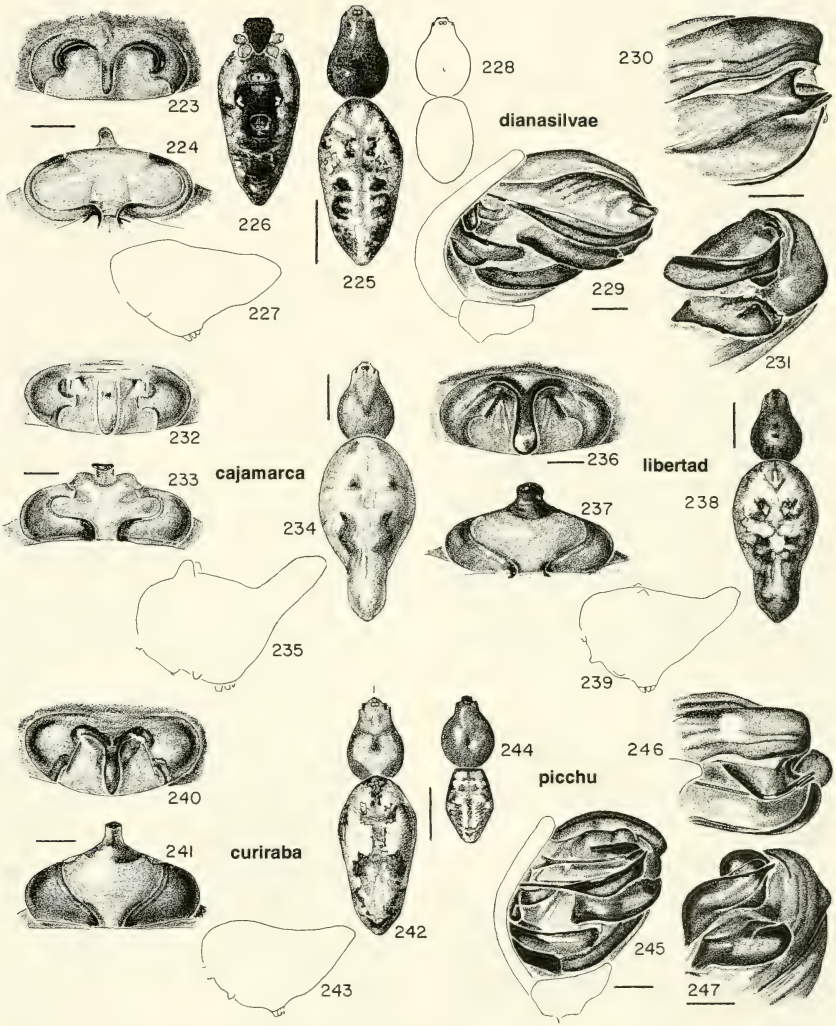
Figures 223–231. *Cyclosa dianasilvae* n. sp. 223–227, female. 223, 224, epigynum. 223, ventral. 224, posterior. 225, dorsal. 226, abdomen, ventral. 227, abdomen, lateral. 228–231, male. 228, dorsal. 229–231, left palpus. 229, mesal. 230, apical. 231, median apophysis.

Figures 232–235. *C. cajamarca* n. sp., female. 232, 233, epigynum. 232, ventral. 233, posterior. 234, dorsal. 235, abdomen, lateral.



Figures 236–239. *C. libertad* n. sp., female. 236, 237, epigynum. 236, ventral. 237, posterior. 238, dorsal. 239, abdomen, lateral.

Figures 240–243. *C. curiraba* n. sp., female. 240, 241, epigynum. 240, ventral. 241, posterior. 242, dorsal. 243, abdomen, lateral.

Figures 244–247. *C. picchu* n. sp., male. 244, dorsal. 245–247, palpus. 245, mesal. 246, apical. 247, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

Cyclosa picchu new species
Figures 244–247; Map 5C

Holotype. Male holotype from Machupicchu, 2,100 m, Depto. Cuzco, Peru, among ruins, 19 Feb. 1965 (H. Levi), in MCZ. The specific name is a noun in apposition after the locality.

Description. Male holotype. Carapace dark brown (Fig. 244). Sternum dark brown. Abdomen venter black with a pair of white patches. Abdomen pointed (Fig. 244). Total length 2.9 mm. Carapace 1.49 mm long, 1.07 wide in thoracic region, 0.41 wide behind posterior lateral eyes. First femur 1.32 mm, patella and tibia 1.39, metatarsus 0.81, tarsus 0.44. Second patella and tibia 1.14 mm, third 0.62, fourth 1.16. Femora shorter than corresponding patellae and tibiae, except third, which is longer.

Variation. Total length of males 2.7 to 2.9 mm. The illustrations were made from the holotype. The holotype has the posterior median eyes fused, apparently an abnormality. The second specimen has all eyes larger than in the holotype and the posterior medians are separate.

Diagnosis. The lobe of the median apophysis of *C. picchu* is fused with the distal tooth (Fig. 247), unlike that of other *Cyclosa*.

Distribution. Peruvian Andes (Map 5C).

Specimens Examined. PERU *Cuzco*: Machupicchu, ruins, bamboo cloud forest, 2,400 m, 16 Oct. 1987, 1♂ (J. Coddington, USNM).

Cyclosa pantanal new species
Figures 248–255; Map 6G

Holotype. Female holotype from Pantanal, Mato Grosso, Brazil, 4–10 Aug. 1992 (A. A. Lise, J. A. Beaul, Jr.), in MNP no. 2337. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace yellowish and brown (Fig. 250). Abdomen venter with black and white patches. Abdomen without dorsal tubercles, but with a median posterior extension (Figs. 250, 251). Total length 5.5 mm. Carapace 1.7 mm long, 1.2 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.8 mm, patella and tibia 1.8, metatarsus 1.1, tarsus 0.4. Second patella and tibia 1.6 mm, third 1.0, fourth 1.7. All femora equal to or slightly shorter than corresponding patellae and tibiae.

Male. Carapace beige, with sides of thoracic region dark gray posteriorly (Fig. 252). Dorsum of abdomen with black, gray and white marks (Fig. 252); venter black with a pair of white patches. Posterior median eyes and laterals slightly smaller than anterior medians. Abdomen oval (Fig. 252). Total length 2.6 mm. Carapace 1.37 mm long, 1.13 wide in thoracic region, 0.42 wide behind posterior lateral eyes. First femur 1.30 mm, patella and tibia 1.23, metatarsus 0.78, tarsus 0.45. Second patella and tibia 0.94 mm, third 0.55, fourth 1.14. Femora slightly longer than corresponding patellae and tibiae.

Note. The association of male and female is uncertain.

Variation. Total length of females 5.2 to 5.5 mm. The illustrations were made from the female holotype.

Diagnosis. *Cyclosa pantanal* is similar to *C. morretes* but differs by lacking dorsal abdominal tubercles (Fig. 250), in having a slightly wider depression on each side of the scape of the epigynum and in having the more sclerotized area in each depression more transverse (Fig. 248) than in *C. morretes* (Fig. 256).

Distribution. Mato Grosso, Brazil (Map 6G).

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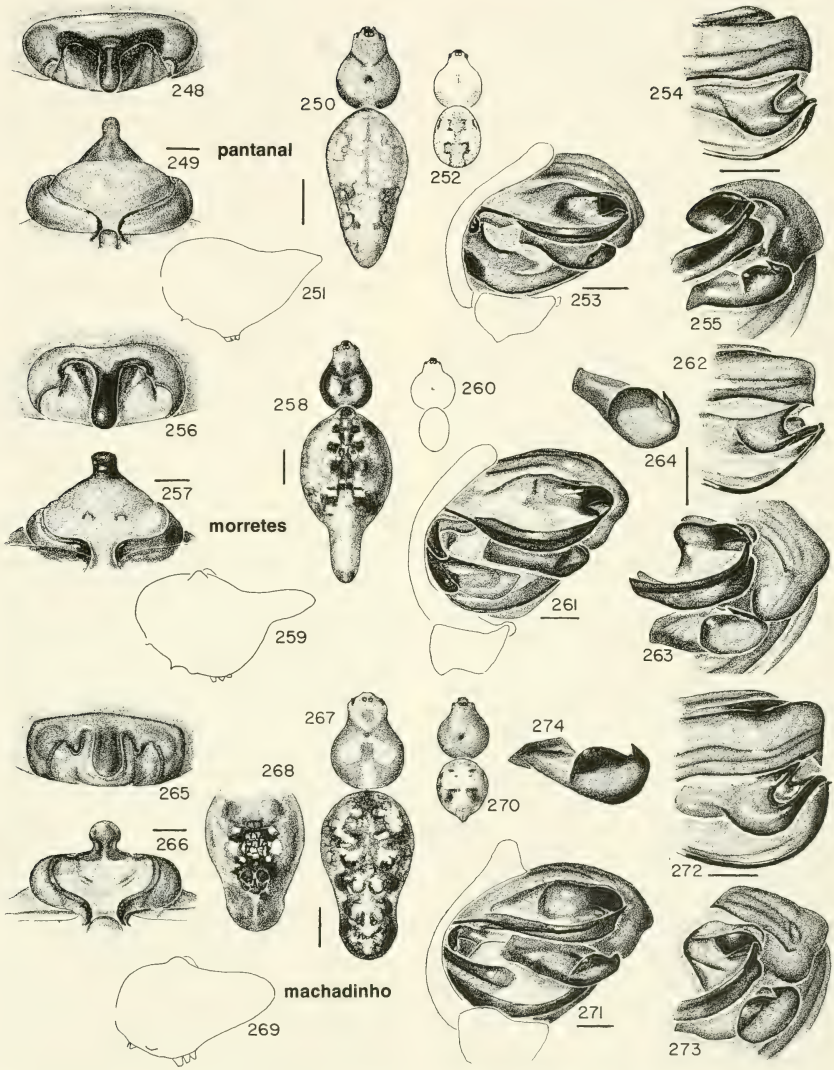
Figures 248–255. *Cyclosa pantanal* n. sp. 248–251, female. 248, 249, epigynum. 248, ventral. 249, posterior. 250, dorsal. 251, abdomen, lateral. 252–255, male (questionable association). 252, dorsal. 253–255, left palpus. 253, mesal. 254, apical. 255, median apophysis.

Figures 256–264. *C. morretes* n. sp. 256–259, female. 256, 257, epigynum. 256, ventral. 257, posterior. 258, dorsal. 259, abdomen, lateral. 260–264, male. 261–264, palpus. 261, mesal. 262, apical. 263, 264, median apophysis.



Figures 265–274. *C. machadinho* n. sp. 265–269, female. 265, 266, epigynum. 265, ventral. 266, posterior. 267, dorsal. 268, abdomen, ventral. 269, abdomen lateral. 270–274, male. 270, dorsal. 271–274, left palpus. 271, mesal. 272, apical. 273, 274, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

Specimens Examined. BRAZIL *Mato Grosso*: Chavantina, Oct. 1946, 1♀ (H. Sick, MZSP 1227); Fazenda Sta. Inês, Poconé, 4–10 Aug. 1992, 1♂ (A. A. Lise, J. A. Beaul, Jr., MCP 2567).

Cyclosa morretes new species
Figures 256–264; Map 6G

Holotype. Female holotype from Morretes, Est. Paraná, Brazil, 28, 29 Oct. 1995 (A. B. Bonaldo), in MCN no. 26727. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace yellow with brown margin, median brown band and groove between cephalic and thoracic region brown (Fig. 258). Sternum colorless with white patches and brown outline. Abdomen venter with black and white patches. Anterior of abdomen stout with a pair of dorsal tubercles and a median posterior extension (Figs. 258, 259). All females have ventral tubercles (Fig. 259). Total length 7.2 mm. Carapace 2.0 mm long, 1.4 wide in thoracic region, 0.8 wide behind posterior lateral eyes. First femur 2.3 mm, patella and tibia 2.4, metatarsus 1.4, tarsus 0.8. Second patella and tibia 2.0 mm, third 1.1, fourth 1.9. All femora about same length as corresponding patella and tibia.

Male from Viamão, Rio Grande do Sul. Carapace dark brown. Distal leg articles orange. Abdomen black with some gray patches on sides. Abdomen with a posterior median point. Total length 2.8 mm. Carapace 1.72 mm long, 1.38 wide in thoracic region, 0.53 wide behind posterior lateral eyes. First femur 1.43 mm, patella and tibia 1.56, metatarsus 1.04, tarsus 0.49. Second patella and tibia 1.33 mm, third 0.83, fourth 1.27.

Males and females were collected together only at Viamão, Brazil (MCN 5866). A female from Pelotas (MCN 28160) was collected with a male of *C. espumoso*.

Variation. Total length of females 5.0 to 7.8 mm, males 2.6 to 3.1. Females occasionally lack the dorsal pair of tubercles. The illustrations were made from female holotype and male from Viamão.

Diagnosis. Females are separated from *C. pantanal* by the shape of the mucus area and depression of the epigynum, more longitudinal in *C. morretes* (Fig. 256) than in *C. pantanal* (Fig. 248). The male is similar to that of *C. pantanal* but differs in the shape of the conductor notch (Fig. 262) and smaller lobe of the median apophysis (Figs. 261, 263). The male differs from that of *C. machadinho* (Fig. 274) by having the median apophysis tooth behind the lobe (Fig. 263).

Distribution. Southern Brazil (Map 6G).

Specimens Examined. BRAZIL *Pará*: Belém, July 1971, 1♀ (T. McGrath, MCZ). *Minas Gerais*: Pedra Azul, Dec. 1970, 1♂ (F. M. Oliveira, AMNH). *Espírito Santo*: Reserva Florestal de Linhares, 28 July 1994, 1♀ (J. Vasconcellos-Neto, MCZ). *Rio de Janeiro*: Angra dos Rais, 1♂ (MZSP 9607); Petrópolis, 1♂ (MNRJ); 2–5 Nov. 1945, 1♀ (H. Sick, AMNH); Rio de Janeiro, Jardim Botânico, 31 Mar. 1987, 1♂ (H., L. Levi, MCZ); Teresópolis, 900–1,000 m, 7–9 Nov. 1945, Mar. 1946, 2♀ (H. Sick, AMNH). *São Paulo*: Bosque da Saúde, 22 Mar. 1942, 1♂ (F. Lane, MZSP 10442); Boroceió, 18 Aug. 1966, 1 imm. (Exped. Depto. Zool., MZSP 5930); Cocaia, Represa Santa Amaro, Sept. 1941, 1♂ (MZSP 2451); 7 Oct. 1948, 4♀ (H. Urban, MZSP 9923); Sept. 1949, 5♀, 5 imm. (H. Urban, MZSP 7856); Eng. Marcilac, 1♀ (P. Biasi, Leme, MZSP 6039); Represa, São Bernardo, 1♂ (MZSP 9605); 1♂ (MZSP 9575); Estr. do Mar, São Bernardo, 7 Feb. 1968, 7♀, 2 imm. (P. Biasi, MZSP 8208, 88217); Ilha São Sebastião, 23 Mar. 1951, 1♀ (H. Urban, MZSP 7217); Santos, 29 Jan. 1951, 1♂ (P. Biasi, MZSP 13152); Jardim Botânico, São Paulo, 9 Mar. 1985, 1♀ (H., L. Levi, MCZ). *Paraná*: Serra da Graciosa, Morretes, 9–20 Jan. 1995, 2♀ (Lab. Arachnol., MCP 6927); Cataratas do Iguaçu, 23–24 Mar. 1985, 1♀ (H., L. Levi, MCZ). *Santa Catarina*: Nova Teutônia, 27°11′S, 52°23′W, 1931, 1♀ (F. Plaumann, SMF); 1 Feb. 1996, 1♂ (A. B. Bonaldo, MCN 27308). *Rio Grande do Sul*: Belém Novo, Porto Alegre, 11 Apr. 1981, 1♀ (A. A. Lise, MCN 9634); Parque Estadual de Caracol, 8 km de Canela, 24 June 1994, 1♀ (M. Ramirez, MACN); Carazinho, 10 Nov. 1979, 1♀ (H. Bischoff, MCN 8660); Floresta Nacional, Paço Fundo, 12 Oct. 1985, 2♀ (A. A. Lise, MCN 13631a); Guíaba, 29 Oct. 1994, 1♀ (A. A. Lise, MCP 5684a); Montenegro, 29 Sept. 1977, 1♀ (E. H. Buckup, MCN 6651a); 3 Nov. 1977, 1♂ (H. A. Gastal, MCN 7152); Pelotas, 31 Dec. 1996, 1♀ (L. Moura, MCN 28160); Rio Pardo, 10 Feb. 1966, 1♀ (A. A. Lise, MCN 0743); Viamão, 21 Dec. 1994, 1♀, 1♂ (MCP 5866); 6 May 1994, 1♀ (A. A. Lise, MCP 4682). ARGENTINA *Misiones*: Montecarlo, Jan. 1966, 4♀ (M. E. Galiano, MACN); Santa María, Oct. 1953, 2♀ (De Carlo, MACN 3890).

Cyclosa machadinho new species
Figures 265–274; Map 6C

Holotype. Female holotype, male allotype, three female and two male paratypes from Machadinho, Rio Grande do Sul, Brazil, 8–14 Feb. 1989 (A. B. Bonaldo), in MCN no. 18181, a pair of paratypes in MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace yellow and brown (Fig. 267). Abdomen venter with black and white patches (Fig. 268). Abdomen with a pair of dorsal tubercles and a median posterior extension (Figs. 267–269) and a pair of ventral tubercles (Fig. 269). Total length 6.8 mm. Carapace 2.4 mm long, 1.8 wide in thoracic region, 1.0 wide behind posterior lateral eyes. First femur 2.3 mm, patella and tibia 2.5, metatarsus 1.4, tarsus 0.7. Second patella and tibia 2.2 mm, third 1.3, fourth 2.4. All femora shorter than corresponding patellae and tibiae.

Male allotype. Carapace brown, cephalic region of carapace lightest (Fig. 270). Abdomen with dorsal black marks (Fig. 270), venter black. Abdomen with posterior median extension and sometimes with anterior tubercles. Total length 3.1 mm. Carapace 1.65 mm long, 1.32 wide in thoracic region, 0.48 wide behind posterior lateral eyes. First femur 1.75 mm, patella and tibia 1.69, metatarsus 1.17, tarsus 0.53. Second femur 1.45 mm, patella and tibia 1.30. Third femur 0.94 mm, patella and tibia 0.78. Fourth femur 1.61 mm, patella and tibia 1.35. All femora longer than corresponding patellae and tibiae.

Note. Males and females were collected together.

Variation. Total length of females 5.5 to 8.3 mm, males 2.8 to 4.0. The illustrations were made from the female holotype and male allotype.

Diagnosis. Unlike all other *Cyclosa* species, *C. machadinho* has the openings in a circular depression facing anteriorly and showing as a loop on each side of the scape (Fig. 265). The male has a conductor notch with parallel sides (Fig. 272), as in *C. tapetifaciens* (Fig. 192), but wider, and the median apophysis tooth is more bent than that of *C. tapetifaciens* (Fig. 194), almost pointing to the attachment of the median apophysis (Fig. 274).

Distribution. Southern Brazil, northern Argentina (Map 6C).

Specimens Examined. BRASIL *Rio de Janeiro*: Petrópolis, 3♀ (AMNH); Teresópolis, 1♀ (AMNH). *São Paulo*: Cocaia, 3♀, 1♂ (MZSP 4654, 9668); Estr. Santos Jurulotuba, 1♀ (MZSP 4704); Campos do Jordão, 1♂ (MZSP 9623); 2♂ (MZSP 13157); Jabaquara, Cidade São Paulo, 1♀ (AMNH); Jequirituba, Cidade São Paulo, 1♀ (AMNH); Guarulhos, 2♀ (MZSP 7299, 8340). *Paraná*: Estância Santa Clara, Guarapuava, 1♀ (MCN 17106); Rincão, 1♀ (MZSP 13156); Rolândia, 1♀ (AMNH); Refúgio Biológica de Santa Helena, Santa Helena, 1♂ (MCN 20837); Serra de Graciosa, Morretes, 1♀ (MCP 7038). *Santa Catarina*: Ilha João da Cunha, Porto Belo, 1♂ (MCP 1635); Volta Grande Concórdia, 1♀ (MCN 19559). *Rio Grande do Sul*: Area de Preservação, Ambiental Celulose, Cambará do Sul, 3♀ (MCN 25985); Cambará do Sul, 2♀ (MCN 24330); 1♀ (MCN 24570); Arvorezinha, 1♀ (MCP 3095); Bage, 6♀ (MCN 9956); Cachoeira do Sul, 1♀, 1♂ (MCN 6020, 6025, MCP 3443); 1♀, 5♂ (MCP 3425, 3426, 3443); Canela, 1♂ (MCN 10149); Canoas, 2♀ (MCN 0288); Fazenda Souza, Caxias, 3♀ (MCP 5323, 7311); Cerro Claro, São Pedro do Sul, 2♀ (MCN 12916); Erechim, Colégio Agrícola, 1♂ (MCN 19571); Erval Grande, 1♂ (MCP 4454); Estreito Augusto Cesar Marcelina Ramos, 1♀ (MCN 19541); Fazenda Coqueiro, Minas Do Leão, 1♀ (MCN 11450); Fazenda São Roque, 1♀ (MCN 11043); Floresta Nacional Passo Fundo, 5♀ (MCN 13631); Guaíba, 2♀ (MCP 5413, 5684); Itaimbenzinho, Cambara do Sul, 2♀ (MCN 12790, 13276); Montenegro, 6♀, 2♂ (MCN 6651, 6752, 7151, 7213, 7526); Novo Hamburgo, 1♂ (MCN 12716); Lomba do Pinheiro, Porto Alegre, 1♂ (MCN 18629); Paso Fundo, 1♂ (MCN 18938); Poço do Carvão, Campo Bom, 1♂ (MCN 8792); Jardim Botânico, Porto Alegre, 1♀ (MCZ); Quaraí, 2♀ (MCP 452); Reserva Florestal, Invernada do Butiá, Ronda Alta, 1♂ (MCN 16056); Santa Maria, 1♂ (MCN 15238); São Francisco de Paula, 2♀ (MCN 9513, MCP 4510); São Valentim, 2♂ (MCN 4789); Banhado das Freiras, São Leopoldo, 1♀ (MCN 27592); Sinodal, São Leopoldo, imm. (MZSP 7186); Parque de Turvo, Tenente Portela, 2♀, 3♂ (MCN 6651, 7213, 8969); Viamão, 1♀ (MCN 0632); Vila Oliva, 1♀ (MCN 00296). PARAGUAY *Boquerón*: Transchaco, km 640, 1♂ (IRSNB). ARGENTINA *Misiones*: San Antonio, 1♀ (MACN 3416); Santa Ana, 1♀ (MACN); Santa María, 2♀, 2♂ (MACN 3588); 2♀ (MACN 2917); Misiones, 1♀ (MACN 1526); Campamento Tobuna [26°28'S, 53°54'W], 1♀ (MACN); 1♀ (AMNH). *Buenos Aires*: Delta del Paraná, Angostura, 2♀ (MACN 1342); Escobar, 2♀ (MACN 2958); Ezeiza, 1♀ (MACN); Isla Martín García, 1♂ (MACN); Paraná de las Palmas,

Canal 6, 7♀ (M. E. Galiano, MACN); Tigre, 1♀ (MACN).

Cyclosa triquetra Simon
Figures 275–283; Map 6D

Cyclosa triquetra Simon, 1895: 779, 782, 784, fig. 851, ♀. Female and male syntypes from Venezuela in MNHN, examined. Roewer, 1942: 760. Bonnet, 1956: 1324.

Cyclosa clara O. P.-Cambridge, 1898: 248, pl. 31, fig. 8, ♀. Ten female and several immature syntypes from Teapa, Tabasco, Mexico, examined. F. O. P.-Cambridge, 1904: 497, pl. 47, fig. 13, ♀. Roewer, 1942: 759. Bonnet, 1956: 1310. NEW SYNONYMY.

Note. As Simon notes behavioral observations, he probably collected specimens himself on his trip to Venezuela.

Description. Female from Costa Rica. Thoracic region of carapace dark brown grading into yellowish cephalic region (Fig. 277). Sternum dark brown with three distinct white patches. Abdomen venter black with a median white patch and adjacent lateral three pairs of white patches (Fig. 278). Abdomen with a pair of tubercles bearing nipples and a median posterior extension (Figs. 277, 279). Total length 3.6 mm. Carapace 1.25 mm long, 1.13 wide in thoracic region, 0.60 wide behind posterior lateral eyes. First femur 1.13 mm, patella and tibia 1.39, metatarsus 0.78, tarsus 0.49. Second patella and tibia 1.17 mm, third 0.65, fourth 1.17. First femora shorter than corresponding patellae and tibiae, second and fourth same length, third longer.

Male from Mala Valley, Peru. Coloration darker than in female, legs brown ringed. Abdomen venter black with one pair of white spots. Abdomen (Fig. 280) as in female. Total length 2.7 mm. Carapace 1.43 mm long, 1.13 wide in thoracic region, 0.48 wide behind posterior lateral eyes. First femur 1.24 mm, patella and tibia 1.32, metatarsus 0.73, tarsus 0.52. Second patella and tibia 1.13 mm, third 0.65, fourth 1.08. First and second femora shorter than corresponding patella and tibia, third and fourth of equal length.

Variation. Total length of females 2.9 to 4.8 mm, males 2.6 to 2.7. Illustrations were made from the female from Costa Rica, and the male from Peru.

Diagnosis. The female can be separated from all others by the shape of the abdomen, almost as long as wide, and by having nipples on the pair of dorsal tubercles (Figs. 277–279). The male has a short abdomen, as in the female, but the nipples are less distinct (Fig. 280). The median apophysis of the palpus has a minute tooth (Fig. 283).

Natural History. Specimens were collected in and around a house and in pasture near Cali, Colombia, and in an apple tree near Mala Valley, Peru. Many collecting sites were relatively dry areas. An egg sac from a Belize female contained only eight eggs.

Distribution. Mexico, Lesser Antilles to Peru and Venezuela (Map 6D).

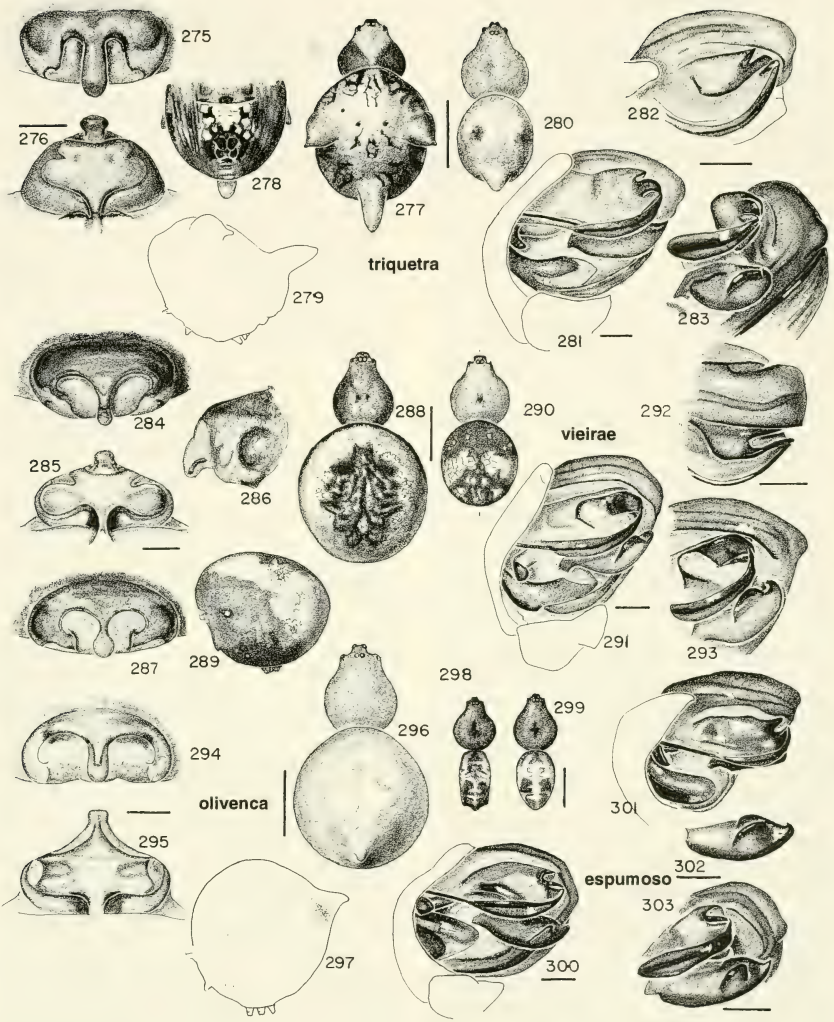
Specimens Examined. MEXICO *Tamaulipas*: Sierra de Tamaulipas, 900 m, 4–7 Aug. 1945, 1♀ (H. Wagner, AMNH). *Yucatan*: Chichen Itza, 16–18 Feb. 1939, 1♂ (AMNH). BELIZE *Stann Creek Distr.*: Twin Cays, 20 Mar. 1986, 1♀; Twin Cays, NW Point, 14 Mar. 1986, 2♀; Twin Cays, Hidden Lake, 19 Mar. 1986, 1♀ (all P. Sierwald, USNM). HONDURAS Tela, 26 July 1929, 1♀ (A. M. Chickering, MCZ). COSTA RICA *Guanacaste*: Tilarán, Dec. 1964, 1♀ (C. E. Valerio, MCZ).

LESSER ANTILLES *Guadeloupe*: Pointe a Pitre, 10, 11 Jan. 1955, 1♀ (A. M. Nadler, AMNH). *St. Lucia*: Castries, Aug. 1976, 1♀ (N. L. H. Krauss,

→

Figures 275–283. *C. triquetra* Simon. 275–279, female. 275, 276, epigynum. 275, ventral. 276, posterior. 277, dorsal. 278, abdomen, ventral. 279, abdomen lateral. 280–283, male. 280, dorsal. 281–283, left palpus. 281, mesal. 282, apical. 283, median apophysis.

Figures 284–293. *C. vieirae* n. sp. 284–289, female. 284–287, epigynum. 284, 287, ventral. 285, posterior. 286, lateral. 284–286, (N of Manaus). 287, (Manaus). 288, dorsal. 289, abdomen lateral. 290–293, male. 290, dorsal. 291–293, palpus. 291, mesal. 292, apical. 293, median apophysis.



Figures 294–297. *C. olivenca* n. sp., female. 294, 295, epigynum. 294, ventral. 295, posterior. 296, dorsal. 297, abdomen lateral.

Figures 298–303. *C. espumoso*, n. sp., male. 298, 299, dorsal. 298, (Salto do Jacuí, Rio Grande do Sul). 299, (Espumosa, Rio Grande do Sul). 301–303, left palpus. 300, mesal. 301, apical. 302, 303, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

AMNH). *Trinidad*: Bayshore, 2 Sept. 1968, 1♀ (R. Jamison, AMNH).

VENEZUELA *Aragua*: Maracay, 15 Feb. 1954, 1♀ (A. M. Nadler, AMNH). COLOMBIA *Córdoba*: Ayapel, nr. Cienaga La Cuajada, 5 Jan. 1987, 1♀ (M. A. Serna, MCZ). *Boyacá*: Muzo, 1936, 2♀ (J. Bequaert, MCZ). *Cundinamarca*: Finca Bella Vista nr. Sasaima, 13–24 May 1965, 3♀ (P. R., D. L. Craig, CAS). *Valle*: nr. Cali, 1,000 m, 28 Feb. 1973, 1♀, 1 imm.; 1 Mar. 1973, 1♀ (H. Levi, MCZ); June 1973, 1♀ (W. Eberhard, 529); Río Vanca nr. Cali, 23 June 1970, 1♀ (W. Eberhard 261, MCZ); Río Cauca nr. Cali, 15. June 1970, 1♀ (W. Eberhard 260, MCZ); Calima, Lago betw. Buga and Loboguerrero, Sept. 1973, 1♀ (W. Eberhard, MCZ). PERU *Piuria*: Quebrada Mogóllon, 30 Apr. 1939, 1♀; 18 June 1939, 1♀; 16 July 1939, 3♀; 24 Sept. 1939, 1♀; Piura Songora, 20 Apr. 1941, 1♀; Pariñas Valley, 7 May 1939, 2♀, 1♂; 21 May 1939, 1♀; Cerra Negro, 15 June 1951, 12 ♀, 4 imm. (all D. L., H. E. Frizzell, CAS). *Lima*: Mala Valley, May 1964, 11♀, 7♂ (CAS).

Cyclosa vieirae new species
Figures 284–293; Map 3B

Holotype. Female holotype from Cabo Frio Reserve, 80 km N Manaus, Est. Amazonas, Brazil, 22 Nov. 1989 (H. Fowler, E. Venticinque, R. S. Vieira), in MCN. The species is named after one of the collectors.

Description. Female holotype. Carapace brown (Fig. 288). Sternum brown. Abdomen with white spots and dark marks, sides dark anteriorly (Figs. 288, 289); venter evenly black, gray anteriorly, with two pairs of white spots, one on each side of pedicel and one on each side in center (Fig. 289). Abdomen spherical in dorsal view without tubercles or posterior extension (Figs. 288, 289). Total length 3.8 mm. Carapace 1.49 mm long, 1.17 wide in thoracic region, 0.57 wide behind posterior lateral eyes. First femur 1.17 mm, patella and tibia 1.33, metatarsus 0.68, tarsus 0.40. Second patella and tibia 1.17 mm, third 0.74, fourth 1.24. All femora shorter than corresponding patellae and tibiae.

Male allotype. Coloration darker than in female. Dorsum of abdomen black anteriorly and posteriorly with white pigment spots between; outline of black areas irregular (Fig. 290); venter as in female. Abdomen (Fig. 290) shape as in female. Total length 3.0 mm. Carapace 1.75 mm long, 1.30 wide in thoracic region, 0.51 wide behind posterior lateral eyes. First femur 1.69 mm, patella and tibia 1.50, metatarsus 1.05, tarsus 0.52. Second patella and tibia 1.16 mm, third 0.73, fourth 1.43. All femora slightly longer than corresponding patellae and tibiae.

Note. Males and females were collected at the same locality, and the spherical abdomen of the male matches that of the female.

Variation. Total length of females 2.6 to 4.2 mm, males 2.7 to 3.0. The illustrations were made from the female holotype and male allotype.

Diagnosis. With its unusual spherical abdomen and dark sides anteriorly, the species could easily be misplaced in *Metazygia*. It is distinguished by its *Cyclosa*-like genitalia, both epigynum (Figs. 284–287) and palpus (Figs. 291–293).

Distribution. Amazon area (Map 3B).

Specimens Examined. PERU *Loreto*: Jenaro Herrera, 04°55′S, 73°45′W, 25 Aug. 1988, 1♀ (D. Silva, MUSM). BRASIL *Amazonas*: 80 km N Manaus, 2°24′S, 59°52′W, 22 Aug. 1989, 2♂, one marked allotype, the other paratype (H. G. Fowler, MCN, MCZ); Cabo Frio Reserve, 6 Sept. 1989, 1♀; 14 Jan. 1990, 2♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ); 14 Jan. 1990, 2♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ); Manaus, Aug. 1971, 1♀ (M. E. Galiano, MACN); Manaus, Reserva Ducke, Aug. 1971, 1♀ (M. E. Galiano, MACN); São Paulo Olivença, 2♀ (M. de Mathan, MNHN 9389).

Cyclosa olivenca new species
Figures 294–297; Map 6B

Holotype. Female holotype from São Paulo de Olivença, Amazonas State, Brazil, pre-1880 (M. de Mathan), in MNHN. The specific name is a noun in apposition after the locality.

Note. Simon recognized the specimen as a *Cyclosa* but did not describe it.

Description. Female holotype with color faded. Prosoma yellow (Fig. 296), distal leg articles indistinctly ringed. Abdomen whitish with indistinct dorsal white folium, lateral white patches and a pair of ventral white pigment patches (Figs. 296, 297). Abdomen spherical with one median, posterior, dorsal tubercle (Figs. 296, 297). Total length 3.6 mm. Carapace 1.30 mm

long, 1.05 wide in thoracic region, 0.73 wide behind posterior lateral eyes. First femur 1.30 mm, patella and tibia 1.30, metatarsus 0.80, tarsus 0.55. Second patella and tibia 1.14 mm, third 0.74, fourth 1.17. Length of femora about same as corresponding patellae and tibiae.

Diagnosis. The abdomen of the female is spherical with a median, posterior tubercle (Fig. 296, 297). It resembles the abdomen of some female theridiids of the genus *Achaearanea* and is unlike any other *Cyclosa* species. However, it has the typical *Cyclosa* epigynum.

Distribution. Known only from the Amazon near the Peruvian border (Map 6D). No other specimens were found.

Cyclosa espumoso new species
Figures 298–303; Map 5B

Holotype. Male holotype from Salto de Jacuí, Espumoso, Rio Grande do Sul, Brazil, 14 Jan. 1982 (A. A. Lise), in MCN no. 9986. The specific name is a noun in apposition after the locality.

Description. Male holotype. Carapace dark brown (Figs. 298, 299). Sternum dark. Abdomen white with dorsal symmetrical dark patches (Figs. 298, 299); venter black. Abdomen with a median posterior point and two posterior tubercles (Figs. 298, 299). Total length 2.9 mm. Carapace 1.53 mm long, 1.13 wide in thoracic region, 0.44 wide behind posterior lateral eyes. First femur 1.12 mm, patella and tibia 1.29, metatarsus 0.78, tarsus 0.48. Second patella and tibia 1.08 mm, third 0.65, fourth 1.14.

Note. The male from Pelotas was collected with the female *C. morretes*, but *C. espumoso* is probably the male of *C. vicente*.

Variation. Total length of males 2.7 to 3.2 mm. Figures 298, 302 illustrate the holotype; Figures 299, 300, 301, 303 are the male from Tenente Portela.

Diagnosis. This male is distinguished from others by the small conductor notch with parallel sides in apical view (Fig. 301) and the asymmetrical median apophysis lobe and its distance from the tooth (Figs. 302, 303).

Distribution. Southern Brazil (Map 5B).

Specimens Examined. BRAZIL *São Paulo*: Jundiaí, Oct. 1976, 1♂ (A. Schneble, MCZ). *Rio Grande do Sul*: Machadinho, 8–14 Feb. 1989, 1♂ (A. B. Bonaldo, MCN 18182); Pelotas, 31 Dec. 1996, 1♂ (L. Moura, MCN 28160); Tenente Portela, 29 Nov. 1978, 2♂ (H. Bischoff, MCN 8438).

Cyclosa monteverde new species
Figures 304–313; Map 6B

Holotype. Female holotype and one female paratype from Monteverde, Guanacaste Prov., Costa Rica, Jan. 1980 (W. Eberhard, 2103), in MCZ. The specific name is a noun in apposition after the locality.

Note. The type and some other specimens are labeled as coming from Guanacaste Province, but Monteverde is in Puntarenas, close to the border with Guanacaste.

Description. Female holotype. Carapace dark brown, cephalic region yellowish (Fig. 306). Abdomen venter black, black around spinnerets (Fig. 307). Abdomen with a pair of anterior tubercles and a median posterior extension (Figs. 306–308). Total length 5.2 mm. Carapace 1.6 mm long, 1.2 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.52 mm, patella and tibia 1.69, metatarsus 0.84, tarsus 0.45. Second patella and tibia 1.43 mm, third 0.8, fourth 1.4. First femora shorter than corresponding patellae and tibiae, others same length.

Male from Cerro Punta, Panama. Prosoma orange, sternum dusky orange. Abdomen black with white patches (Fig. 309), venter black with one pair of white patches. Abdomen as in female, tubercles less distinct (Fig. 309). Total length 2.4 mm. Carapace 1.30 mm long, 1.07 wide in thoracic region, 0.40 wide behind posterior lateral eyes. First femur 1.17 mm, patella and tibia 1.26, metatarsus 0.68, tarsus 0.36. Second patella and tibia 0.99 mm, third 0.54, fourth 0.92.

Note. A male was collected with females at Cerro Punta, Panama.

Variation. Total length of females 3.8 to

5.2 mm. The illustrations were made from the female holotype and the male from Cerro Punta.

Diagnosis. Cyclosa monteverde has the body shape of *C. turbinata*, except that the posterior end of the abdomen is narrower (Figs. 306, 308). The epigynum differs from that of *C. turbinata* (Fig. 314) by having a narrower scape; each side of the epigynum could be covered by three or more widths of the scape (Fig. 304), whereas in *C. turbinata*, each side of the epigynum could be covered by only two widths of the scape (Fig. 314). The median apophysis of the *C. monteverde* palpus differs by having a distinct, distal keel and a more proximal tooth on the median apophysis (Figs. 312, 313), whereas in *C. turbinata*, the keel fades out toward the tooth (Fig. 321).

Distribution. Costa Rica and western Panama (Map 6B).

Paratypes. COSTA RICA *Puntarenas*: Monteverde, 13 Oct. 1961, 22♀ (C. W. Parker, AMNH); Jan 1980, 4♀ (W. Eberhard 2100–2102, 2104, MCZ).

Specimens Examined. COSTA RICA *Puntarenas*: Monteverde, 1,500 m, Jan. 1983, 1♀ (W. Eberhard, MCZ); Monteverde Community, San Luis Road, 1,450 m, 29 Nov. 1976, 1♀ (C. L. Craig, MCZ). *San José*: Cerro de Escazú, 1,500 m, Oct. 1987, 1♀ (W. Eberhard SA4 105, MCZ); Río Hondura, 1,200 m, Nov. 1987, 1♀ (W. Eberhard SAE-233, MCZ). *Cartago*: Cartago, 4♀ (N. Banks, MCZ). PANAMA *Chiriquí*: Cerro Punta, 4 Mar. 1936, 14♀, 1♂; El Volcán, 28 Feb. 1936, 1♀ (both W. J. Gertsch, AMNH).

Cyclosa turbinata (Walckenaer) Figures 314–321; Map 6A

Epeira turbinata Walckenaer, 1841: 140. Description of female figures 79, 80 from Georgia in Abbot's Georgia Spiders manuscript kept in BMNH. Copy of manuscript in MCZ, examined.

Epeira caudata Hentz, 1850: 23, pl. 3, fig. 14, ♀. Female types from the USA in the Boston Natural History Museum, destroyed. First synonymized by McCook 1894: 224.

Cyclosa index O. P.-Cambridge, 1889: 51, pl. 6, fig. 6, ♀. Female holotype from Tamahú, Guatemala in BMNH, examined. F. P.-Cambridge, 1904: 496, pl. 47, fig. 12, ♀. First synonymized by Levi (1977).

Cyclosa turbinata:—McCook, 1894: 224, pl. 17, figs. 5, 6, ♀, ♂. Petrunkevitch, 1911: 334. Roewer, 1942: 761. Bonnet, 1956: 1325. Levi, 1977: 80, pl. 2, figs. 20, 38–50, map 2.

Cyclosa caudata:—Keyserling, 1893: 279, pl. 14, fig. 206, ♀, ♂.

Cyclosa culta O. P.-Cambridge, 1893: 112, pl. 14, fig. 12, ♂. Two male syntypes, both with left palpus lost in 1997, from Omilteme, Guerrero, Mexico, in BMNH, nos. 1905.4.28.2844–5, examined. F. P.-Cambridge, 1904: 493, pl. 47, fig. 2, ♂. First synonymyzed by Levi (1977).

Cyclosa tuberculifera O. P.-Cambridge, 1898: 269, pl. 36, fig. 10, ♂. Male holotype without palpi from Teapa, Tabasco, Mexico, in BMNH, no. 1905.4.28.2843, examined. F. P.-Cambridge, 1904: 493, pl. 47, fig. 1, ♂. Roewer, 1942: 761. Bonnet, 1956: 1325. Doubtful synonymy by Levi (1977).

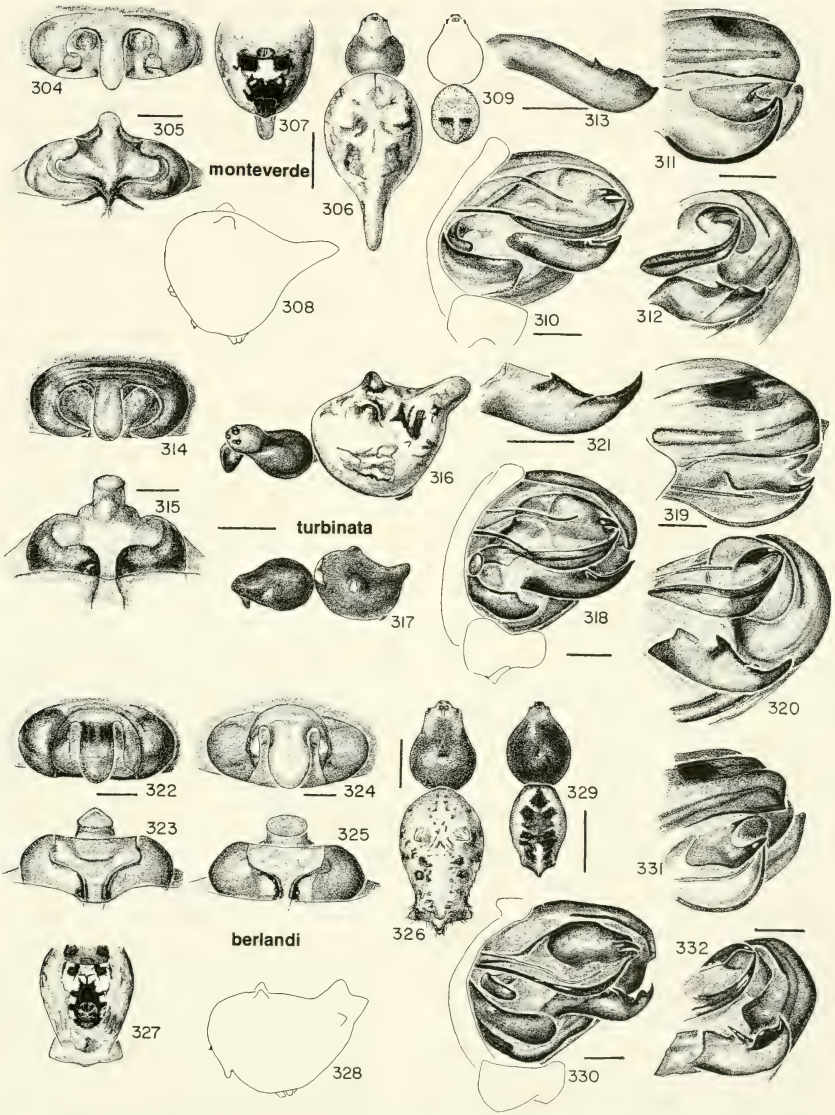
Description. Female from Isla Raza, Gulf of California. Carapace dark brown grading into yellowish cephalic region (Fig. 316). Abdomen venter black with three pairs of white patches, the median pair largest. Abdomen with a pair of humps and a median posterior extension (Fig. 316). Total length 4.4 mm. Carapace 1.6 mm long, 1.2 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.4 mm, patella and tibia 1.6, metatarsus 0.9, tarsus 0.4. Second patella and tibia 1.4 mm, third 0.9, fourth 1.4. Femora shorter than corresponding patellae and tibiae, except third, which is longer.

Male from Isla Raza, Gulf of California. Coloration much darker than in female. Abdomen black with three white patches dorsally; venter black with one pair of white patches (Fig. 317). Abdomen (Fig. 317) as in female. Total length 3.2 mm. Carapace 1.60 mm long, 1.20 wide in thoracic region, 0.47 wide behind posterior

→

Figures 304–313. *Cyclosa monteverde* n. sp. 304–308, female. 304, 305, epigynum. 304, ventral. 305, posterior. 306, dorsal. 307, abdomen, ventral. 308, abdomen, lateral. 309–313, male. 309, dorsal. 310–313, left palpus. 310, mesal. 311, apical. 312, 313, median apophysis.

Figures 314–321. *C. turbinata* (Walckenaer). 314–316, female. 314, 315, epigynum. 314, ventral. 315, posterior. 316, sublateral. 317–321, male. 217, sublateral. 318–321, palpus. 318, mesal. 319, apical. 320, 321, median apophysis.



Figures 322–332. *C. berlandi* n. sp. 322–328, female. 322–325, epigynum. 322, 324, ventral. 323, 325, posterior. 322, 323, (Mexico). 324, 325, (Ecuador). 326, dorsal. 327, abdomen, ventral. 328, abdomen, lateral. 329–332, male. 329, dorsal. 330–332, palpus. 330, mesal. 331, apical. 332, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

lateral eyes. First femur 1.47 mm, patella and tibia 1.43, metatarsus 0.74, tarsus 0.44. Second patella and tibia 1.17 mm, third 0.73, fourth 1.24. All femora slightly longer than corresponding patella and tibia.

Note. Males and females were collected together.

Variation. Total length of females 3.6 to 5.0 mm, males 2.5 to 3.6. Some females lack humps. The illustrations were made from female specimens from Isla Raza, and the male from Venado Arroyo [Mexican locality not located].

Diagnosis. The shape of the abdomen separates this species from *C. walckenaeri* (Fig. 337) and the epigynum has a wider scape (Fig. 314) than that of *C. monteverde* (Fig. 304). The palpus of the male (Figs. 318–321) is similar to that of *C. walckenaeri* (Figs. 340–342), but the shape of the abdomen (Fig. 317) usually differs.

Natural History. Specimens have been found on mangroves in Baja California, tidepool beach in Sonora.

Distribution. From New England and Washington State south to Panama, Bermuda, Greater Antilles and Galapagos (Map 6A).

Specimens Examined. BERMUDA July 1904, 7♀, 1♂ (J. Kincaid, CAS); Dyer Island, 25 June 1918, 2♀, 1♂ (MCZ); Grasmere, 10 July–4 Aug. 1921, 2♂ (E. B. Bryant, MCZ).

MEXICO Venado Arroyo [?], 27 July 1934, 1♂ (MCZ). *Chihuahua*: Matachic, 6 July 1947, 1♀ (W. J. Gertsch, AMNH). *Nuévo León*: Horsetail Falls, San Juan River Canyon, 1 Aug. 1968, 1♀ (J. E. Carico, USNM). *Chihuahua*: Creel, 27°45′N, 107°38′W, 6 July 1991, 2♀ (W. H. Piel, G. S. Bodner, MCZ). *Sonora*: 15 to 20 km E Brevicora, 29°43′N, 110°05′W, 6 Aug. 1983, 1♀ (V. B. Roth, CAS); Puerto Kino, Dec. 1963, 1♀ (W. Eberhard, MCZ); S Puerto Libertad, 4 Nov. 1983, 1♀, 3♂ (V. Roth, CAS); Topaca Bay, 29 Apr. 1921, 3♀ (J. C. Chamberlin, MCZ); El Coyote, 28 km E Río Bavispe, 20 July 1980, 1♂ (J. A. Beatty, AMNH). *Baja California Norte*: Isla Partida, 22 Apr. 1921, 1♀; 1 July 1921, 4♀ (both J. C. Chamberlin, MCZ); 24 km S Punta Prieta, 7 July 1973, 1♀ (S. C. Williams, K. B. Blair, CAS); Rancho Las Parritas, 16 km S. San Quintin, 27, 28 June 1977, 4♀ (C. E. Griswold, CAS); Isla Raza, 21 April 1921, 4♀, 1♂ (J. C. Chamberlin, MCZ); May to July 1921, 2♀ (J. C. Chamberlin, CAS); Isla Partida, 1 July 1921, 6♀ (J. C. Chamberlin, CAS). *Baja California Sur*: 50 km S La Laguna, 30 June 1968, 1♂ (H. Bentzien, CAS); Santiago, 18 Mar. 1944, 1♂ (AMNH); La Paz, 12 Apr. 1921, 1♀ (J. C. Chamberlin, MCZ); 8 km S Miraflores, road to Las Casitas, 15 Dec. 1977, 1♀ (L. Vincent, C. E. Griswold, CAS); Aldefano Isl., 17, 18 May 1921, 1♀, 1♂ (J. C. Chamberlin, MCZ); Las Galnas Island, 14 June 1921, 2♀ (J. C. Chamberlin, MCZ); Santa Lucy Isl., 13 May 1921, 2♀ (J. C. Chamberlin, MCZ). *San Luis Potosí*: 46 km S Huizache, 4 July 1985, 1♂ (J. B. Woolley, G. Zolnerowich, AD); 3 km W Pilares, 21°55′N, 100°48′W, 21 Oct. 1994, 1♀ (W. H. Piel, MCZ). *Durango*: Palos Colorados, 2,400 m, 5 Aug. 1947, 6♀ (W. J. Gertsch, AMNH); Otinapa, 2,500 m, 12 Aug. 1947, 1♀ (W. J. Gertsch, AMNH). *Jalisco*: 11 km S Mazamitla, 1 Dec. 1948, 1♀ (H. B. Leech, CAS). *Puebla*: Huauchinango, 7 Oct. 1947, 1♂ (H. M. Wagner, AMNH); 6 km S Zacapoaxtla, 23 July 1985, 2♂ (J. Woolley, AD). *Guerrero*: 8 km SW Filo de Ceballo, 17 July 1984, 1♂ (J. B. Woolley, AD). *Yucatan*: 12 km S Muna on Highway 261, 20°24′N, 89°48′W, 21 July 1983, 1♂ (W. Maddison, MCZ). COSTA RICA *Cartago*: Cartago, 4♀ (Tristam, MCZ). PANAMA *Chiriquí*: Boquete, July 1939, 1♀; Aug. 1950, 4♀ (A. M. Chickering, MCZ); El Volcán, Aug. 1950, 2♀ (A. M. Chickering, MCZ).

CUBA *Havana*: Santiago de las Vegas, Apr. 1967, 2♀ (P. Aloyo, MCZ). *Pinar del Río*: Pinar del Río, 1♂ (J. Caraboa, MCZ). HAITI 32 km NW of Las Cayes, Les Platons, 750 m, July 1972, 1♀ (T. Moermond, MCZ); Las Cayes, Les Platons, Nov. 1971, 1♀ (T. Moermond, MCZ). LESSER ANTILLES *St. Kitts*: Windfield River, 30 May 1927, 2♀ (Roys, MCZ).

GALAPAGOS ISLANDS 18 May 1899, 2♀ (AMNH); Champion Isl., 1♀, (Y. Lubin, MCZ); Española Isl., 5 June 1983, 1♀ (Y. Lubin, MCZ); Fernandina Isl., 3 km inland, 25–27 Mar. 1970, 1♂ (R. Silberglied, MCZ); Cabo Hammond, Fernandina Isl., 15 Oct. 1982, 3♀, 3♂ (Y. Lubin, MCZ); Santa Cruz Island, 21 Apr. 1981, 1♂ (Y. Lubin, MCZ); S coast, Santa Fé Isl., 28 Jan. 1983, 1♀ (Y. Lubin, MCZ); SE Los Guayabilles, Santiago Isl., 15–20 Mar. 1983, 1♂ (Y. Lubin, MCZ); Albomarle, 2 Feb. 1899, 3♀ (AMNH); 14 Feb. 1899, 6♀ (AMNH); 13 Feb. 1899, 1♂ (AMNH); Lagus Cove, 13 Jan. 1899, 3♂ (AMNH); Narborough, 7 Apr. 1899, 1♀ (AMNH).

Cyclosa berlandi new name
Figures 322–332; Map 7B

Holotype. Female neotype and male from 20 km N Cuenca, 2,200 m, Ecuador (L. Peña), in MCZ.

Cyclosa trituberculata Berland, 1913: 91, pl. 9, figs. 36–41, ♂. Male holotype from Pinllar, Ecuador, lost. *Cyclosa trituberculata* is a homonym of a name by Lucas, described as *Epeira trituberculata* Lucas, 1846: 248. The Lucas name was placed in *Cyclosa* by Simon, 1874: 43.

Note. Berland described spiders from the mountains of Ecuador, illustrated the abdomen of the male, with three posterior

tubercles and a nondiagnostic view of the male palpus. As there is only one common species in the area with triforked abdomen in males; the identification is easy. The locality Pinllar has disappeared from recent gazetteers; it is northwest of 0°, 78°W (American Geographical Society, 1944).

The Lucas name *Cyclosa trituberculata* has been synonymized with *C. insulana* (Costa) (Roewer, 1942: 755).

Description. Female neotype. Carapace dark brown, cephalic region yellowish (Fig. 326). Abdomen (Fig. 326); venter black around spinnerets with white patches between epigynum and spinnerets (Fig. 327). Abdomen with six tubercles (Figs. 326–328). Total length 4.2 mm. Carapace 1.7 mm long, 1.1 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.4 mm, patella and tibia 1.6, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.4 mm, third 0.7, fourth 1.4. Femora of second and fourth legs same length as corresponding patellae and tibiae, third slightly longer.

Male collected with neotype. Coloration as in female. Dorsum of abdomen with contrasting markings (Fig. 329), venter black with one pair of white patches. Abdomen with three posterior tubercles (Fig. 329). Total length 3.0 mm. Carapace 1.56 mm long, 1.20 wide in thoracic region, 0.44 wide behind posterior lateral eyes. First femur 1.43 mm, patella and tibia 1.33, metatarsus 0.81, tarsus 0.48. Second patella and tibia 1.11 mm, third 0.66, fourth 1.08. All femora are longer than corresponding patellae and tibiae.

Note. Males and females were collected together.

Variation. Total length of North and Central American females 4.3 to 6.5 mm, males 2.8 to 3.9. Total length of South American females 4.2 to 6.0 mm, males 2.8 to 3.8. There is some doubt that the North American specimens are the same species as those from Colombia and Ecuador. Figures 322, 323, 327, 328 illustrate a female from Mexico; Figures 324, 325 the female neotype; Figure 326 from northern Colombia; Figure 330 from Mexico; Figures 329, 331, 332 a male from Ecuador.

Diagnosis. The female has a wider, shorter scape (Fig. 322) and a smaller posterior median plate (Figs. 323, 325) than *C. walckenaeri* (Figs. 334, 336). The male differs by having a lobe and tooth on the median apophysis (Figs. 330, 332), whereas *C. walckenaeri* has a keel (Figs. 340, 343).

Distribution. The distribution is California, Texas, Mexico, Central America to Ecuador and Hispaniola (Map 7B). In 1977 I confused specimens of this species with the similar *C. walckenaeri*. Records of *C. walckenaeri* from California (Levi, 1977) are actually for this species.

Specimens Examined. UNITED STATES *Texas*: *Big Bend National Park*: Chisos Mountains, 28 Sept. 1950, 1♀ (W. J. Gertsch, AMNH). *California*: *Monterey Co.*: Carmel, Sept.–Oct. 1945, 1♀ (A. F. Archer, AMNH); Monterey, Aug., Sept. 1945, 11♀, 1♂ (A. F. Archer, AMNH); Del Monte Forest, 2.3 km S Pacific Grove, 8 Oct. 1945, 1♀ (A. F. Archer, AMNH). *Santa Cruz Co.*: Felton, St. Cruz Mts, 22 May 1907, 1♂ (J. C. Bradley, AMNH). *San Luis Obispo Co*: Cambria, 29 June 1957, 1♀ (J. G. Edwards, MCZ). MEXICO Arroyo Venado [?], 27 July 1934, 4♀, 1♂ (MCZ). *Nuévo León*: Chepinque nr. Monterrey, 7 Apr. 1946, 1♀, 1♂ (A. M., L I. Davis, AMNH). *Coahuila*: 14 km N Saltillo, 24 May 1952, 1♂ (M. Cazier et al., AMNH). *Chihuahua*: Madera, 5 July 1947, 2♀ (W. J. Gertsch, AMNH); Pelayo, 100 km W Santa Barbara, 20 July 1947, 1♀ (W. J. Gertsch, AMNH). *Sonora*: 24 km S Navoja, 8 Apr. 1979, 1♂ (D. G. Denning, AMNH). *Baja California Sur*: 12 km W Santiago, Rancho Mata Gorda, 18 Dec. 1977, 1♀ (C. Griswold, L. Vincent, CAS). *San Luis Potosí*: Tamazunchale, 19 Apr. 1963, 1♀ (W. J. Gertsch, W. Ivie, AMNH); 4.5 km E San Francisco, Rt. 70, 26 May 1982, 1♀ (F. Coyle, MCZ). *Zacatecas*: Guadalupe, 16 Aug. 1947, 1♂ (W. J. Gertsch, AMNH); E Guadalupe, 21 Aug. 1959, 4♀, 1♂ (A. F. Archer, AMNH). *Durango*: Palos Colorados, 2,600 m, 5 Aug. 1947, 2♀ (W. J. Gertsch, AMNH). *Querétara*: 3.2 km E Final de Amoles, Rt. 120, 27 May 1982, 1♀ (F. Coyle, MCZ). *Guanajuato*: 3.2 km W Dolores, Hidalgo, 5 July 1985, 1♂ (J. Woolley, G. Zolnerowich, AD 85/026); 48 km NE León Guanajuato, 10 km SE Silco, 20°52′N, 101°21′W, 6 Sept. 1964, 1♀ (J., W. Ivie, AMNH). *Jalisco*: 19 km. S Mazamitla, 5 Dec. 1948, 1♂ (E. S. Ross CAS); 4.8 km S Mazamitla, 10 May 1963, 1♀, 2♂ (W. J. Gertsch, W. Ivie, AMNH). *Veracruz*: 25 km W Jalapa, 29 July 1955, 3♀, 2♂ (C. P. Vaurie, AMNH); 24 km W Jalapa, 23 June, 3♀ (A. M., L. I. Davis, AMNH);

Perote, 29 July 1955, 3♀, 2♂ (C., P. Vaurie, AMNH); Orizaba, 1♂ (Crawford Coll, MCZ). *Hidalgo*: Alfajayucan, Ixmiquilpan, 22 Aug. 1947, 1♂ (H. Wagner, AMNH); Apulco, 6 Oct. 1947, 1♀ (H. M. Wagner, AMNH); Ixmiquilpan, 15 Aug. 1947, 1♀, 1♂ (H. Wagner, AMNH); Tenango, 5 Oct. 1947, 5♀ (H. M. Wagner, AMNH). *México*: Tenancingo, 7–15 Sept. 1946, 1♀ (H. M. Wagner, AMNH); San Juan Teotihuacan, 3 July 1941, 1♀ (L. I. Davis, AMNH). *Michoácan*: mountains above Morelia, 24 Aug. 1958, 1♀ (A. F. Archer, MCZ); Tepetates Pass, 24 km W Hidalgo, 8 May 1963, 1♀, 2♂ (W. J. Gertsch, W. Ivie, AMNH). *Puebla*: 8 km SE Izucar de Matamoras, 20 July 1984, 1♂ (J. B. Woolley, MCZ); Tehuacan, 17–24 Oct. 1944, 1♀ (H. Wagner, AMNH); Cholula, 1975, 1♀ (A. F. Archer, AMNH). *Morelos*: Cuernavaca, Oct. 1944, 1♀ (N. L. H. Krauss, AMNH). *Guerrero*: W Chilapa, 16 July 1984, 1♂ (J. Woolley, AD 84/036). *Oaxaca*: Huajuapan, 27 Sept.–1 Oct. 1946, 1♂ (H. Wagner, AMNH); S Balt. Chichicapan, 4 Aug. 1991, 1♀ (W. H. Piel, G. S. Bodner, MCZ); 6 mi NE Mitla, 20 July 1985, 1♂ (J. Woolley, G. Zolnerowich, AD 85/077); Huamatla, July 1981, 1♀ (G. Gold, CAS). *Tabasco*: coast, July 1981, 1♀ (G. Gold, CAS). *Chiapas*: San Cristobal de las Casas, 22 July 1947, 1♂ (C.,M. Goodnight, AMNH); 11 Sept. 1947, 7♀, 2♂; 13 Sept. 1947, 2♀, 1♂ (H. Wagner, AMNH); 31 Dec. 1974, 3♀ (P. R. Craig, D. Green, CAS); 8 km W San Cristobal, 16°45′N, 92°41′W, 24 Aug. 1966, 2♀ (J. W. Ivie, AMNH). GUATEMALA Chichicastenango, 6, 7 Aug. 1947, 2♂ (C., P. Vaurie, AMNH); Ciudad Guatemala, 20 Aug. 1947, 1♀ (B. Malkin, AMNH); Nebaj, 9, 10 Aug. 1947, 1♂ (C., P. Vaurie, AMNH). COSTA RICA Chiral Paraiso [?], 1♀ (Biolley and Tristan, MCZ). *San José*: Cerro de Escazú, 1,500 m, Oct. 1987, 1♀ (W. Eberhard, MCZ). PANAMA *Chiriquí*: Boquete, July 1939, 2♀, 1♂; 4–11 Aug. 1954, 3♀, 1♂ (A. M. Chickering, MCZ); El Volcán, 9–14 Aug. 1950, 1♀, 1♂ (A. M. Chickering, MCZ).

HISPANIOLA *Santa Domingo*: La Altagracia, Punta Cana, Isla Saona, 24 July 1992, 1♀ (F. Del Monte, K. Guerrero, Del Monte Coll.).

COLOMBIA *Magdalena*: San Sebastián de Rábago, 2,000 m, Sierra Nevada de Santa Marta, 1–10 Apr. 1968, 4♀ (B. Malkin AMNH). *Cundinamarca*: Tomine Dam, 2,600 m, 24 July 1988, 1♀ (C. Valderrama, CV). ECUADOR *Pichincha*: Mt. Pichincha, Aug. 1944, 2♀ (C. W. Prescott, MCZ); Quito, 22 Apr. 1942, 2♀ (H. E. Frizzell, CAS); Tumbaco, 14 Oct. 1989, 2♀ (L. Avilés, MECN). *Tungurahua*: Ambato, 9–11 June 1943, 45♀, 11♂ (H. E., D. L. Frizzell, CAS); Ambato region, 1 Sept. 1992, 1♀ (W. Piel, D. Fitzpatrick, Estevez, MECN); Baños, 1,800 m, Oct. 1937, 4♀ (W. Clarke, W. C. Macintyre, AMNH); 10 Apr. 1939, 1♂ (W. C. Macintyre, MCZ); 7 May 1942, 17♀, 3♂ (H. E. Frizzell, CAS); 15–21 June 1943, 50♀, 24♂ (H. E., D. L. Frizzell, CAS); Baños, Río Pastaza, 1,800 m, 4 Apr. 1958, 5♀ (W. Weyrauch, CAS); Pastaza Valley, between Baños and Nero, 1,000–1,700 m, Jan.–Mar. 1949, 1♀ (W. Clarke, W. C. Macintyre, AMNH); Puñapi, 19 June 1943, 30♀, 6♂ (H. E., D. L. Frizzell, CAS). *Bolívar*: Echeandía (Ontongo), 1989, 1♀ (G. Estévez, MECN). *Azuay*: Cuenca, 3 Apr. 1942, 21♀, 12♂ (H. E. Frizzell, CAS); S of Cuenca, 2,500–2,800 m, 15 Mar. 1965, 1♂ (L. Peña, MCZ); Lago Zurucucha, W Cuenca, 16 Feb. 1955, 2♀, 2♂ (E. I. Schlinger, E. S. Ross, CAS).

Cyclosa walckenaeri (O. P.-Cambridge) Figures 333–343; Map 7A

Turckheimia walckenaerii O. P.-Cambridge, 1889: 47, pl. 8, fig. 6, ♀. Three female syntypes from Volcán de Fuego, Guatemala, in BMNH, examined in 1968. The specimen has since been lost.

Epeira walckenaeri Keyserling, 1892: 98, pl. 5, fig. 85, ♀. Eleven female syntypes from Bogota, Colombia, in BMNH no. 1890.7.1.5004–5015, examined. The syntypes belong to three species and a lectotype is here designated. The paralectotypes included 4♀ *C. walckenaeri*, 5♀ *C. berlandi* and 1♀, 1 imm. *C. bifurcata*, 1 imm. (not determined).

Cyclosa walckenaeri:—F. P.-Cambridge, 1904: 495, pl. 47, fig. 9, ♀. Roewer, 1942: 761. Bonnet, 1956: 1326. Levi, 1977: 84, pl. 4, figs. 64–77, ♀, ♂, map 2. Species first placed in *Cyclosa* by McCook, 1894: 226, pl. 17, figs. 1, 2.

Cyclosa trifida F. P.-Cambridge, 1904: 495, pl. 47, fig. 7, ♀. Three female syntypes, slightly damaged, from Cohabon [Cahabón, Selander and Vaurie, 1962], Guatemala, in the BMNH 1905.4.28.2864–7, examined. First synonymized by Levi (1977).

Cyclosa cuadrituberosa Franganillo, 1936: 84. Immature, male holotype in ACCH, examined. Franganillo's immature specimens appear to lack lateral posterior tubercles. First synonymized by Levi (1977).

Cyclosa oculata:—Bryant, 1940: 259, 337; Bryant 1942: 346; Bryant 1945: 367. Misidentification.

Cyclosa quadrituberosa:—Roewer, 1954: 1454. Bonnet, 1956: 1322 (unjustified name corrections).

Note. I made illustrations of *Turckheimia walckenaerii* types in 1968 when visiting the BMNH. My note indicating that the three syntypes are variable, suggests

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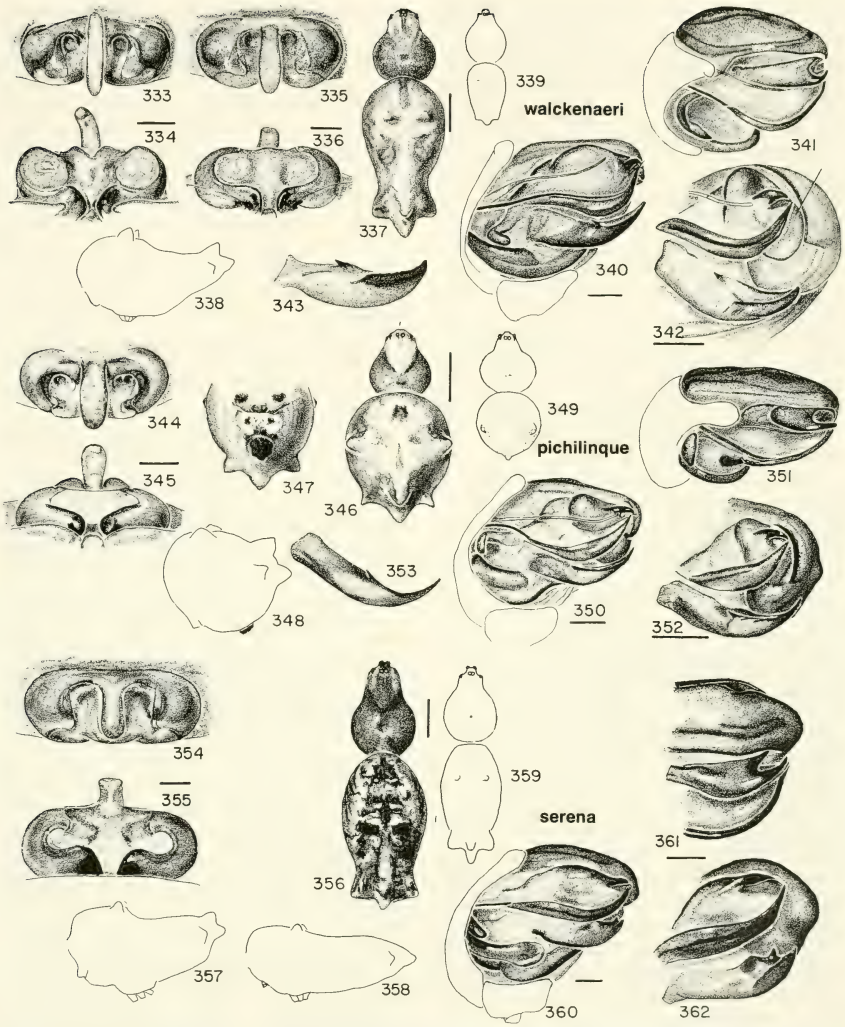
Figures 333–343. *Cyclosa walckenaeri* (O. P.-Cambridge). 333–338, female. 333–336, epigynum. 333, 335, ventral. 334, 336, posterior. 333, 334, (Yucatan, Mexico). 335, 336, (Tortola Isl., Virgin Islands). 337, dorsal. 338, abdomen, lateral. 339–343, male. 339, dorsal. 340–343, left palpus. 340, mesal. 341, apical. 342, 343, median apophysis.



Figures 344–353. *C. pichilinque* n. sp. 344–348, female. 344, 345, epigynum. 344, ventral. 345, posterior. 346, dorsal. 347, abdomen, ventral. 348, abdomen, lateral. 349–353, male. 349, dorsal. 350–353, palpus. 350, mesal. 351, apical. 352, 353, median apophysis.

Figures 354–362. *C. serena* n. sp. 354–358, female. 354, 355, epigynum. 354, ventral. 355, posterior. 356, dorsal. 357, 358, abdomen, lateral. 357, (Chile). 358, (Argentina). 359–362, male. 359, dorsal. 360–363, palpus. 360, mesal. 361, apical. 362, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

that a lectotype should be chosen, but the specimens have since been lost.

The types of *Epeira walckenaeri* Keyserling included 11 specimens; some may have been added at a later time. It included an original 2- by 4-cm label with perforation teeth, a 15- by 35-mm blue frame and a faded penciled note: "Sta. Fé de Bogota, Epeira (Cyclosa) walck . . . aeri Keys" with most of the specific name faded. The Keyserling illustrations are of *C. walckenaeri* (O. P.-Cambridge), recognized by the narrow scape with parallel sides. Paratypes of this species, examined from Taquara do Mundo Novo, Rio Grande do Sul, Brazil, BMNH 1890.7.1.5015–6, are *C. bifurcata* (Walckenaer).

The carapace of *Cyclosa cuadrituberosa* specimen is 1.05 mm total length; the abdomen is missing.

Miss Bryant requested a specimen of *Cyclosa oculata* (Walckenaer), identified by Simon, from the Paris museum. However, the specimen she received came from the Dominican Republic, not the type locality (near Paris); furthermore, it was a specimen of *C. walckenaeria*, misidentified by Simon as *C. oculata* because of a similar abdomen. Miss Bryant (1940) published on this Dominican Republic specimen, and subsequently (before Levi, 1977) all American specimens having six tubercles on the abdomen were misidentified.

Description. Female from Chichen Itza. Carapace dark brown, cephalic region lighter (Fig. 337). Abdomen venter with various size black and white patches. Abdomen with anterior pair of tubercles, a posterior pair and two posterior tubercles in median line (Figs. 337, 338). Total length 5.8 mm. Carapace 2.1 mm long, 1.5 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.8 mm, patella and tibia 2.0, metatarsus 1.1, tarsus 0.5. Second patella and tibia 1.7 mm, third 1.0, fourth 1.6. Femora shorter than corresponding patellae and tibiae, except third, which is of same length.

Male from Campeche. Much darker than female. Prosoma blackish brown. Abdomen black with a pair of dorsal white spots. Abdomen narrower than that of female (Fig. 339). Total length 2.8 mm. Carapace 1.75 mm long, 1.32 wide in thoracic region, 0.51 wide behind posterior median eyes. First femur 1.46 mm, patella and tibia 1.69, metatarsus 1.59, tarsus 0.60. Second patella and tibia 1.25 mm, third 0.70, fourth 1.30. First femora shorter than corresponding patellae and tibiae, others slightly longer.

Note. Males and females were collected together.

Variation. Total length of females 4.0 to 7.6 mm; males 2.7 to 4.8. Larger males may have a wider abdomen than the one illustrated and have a pair of anterior dorsal humps. Figures 333, 334, 337 illustrate a female from Yucatan; Figures 335, 336, 338 from Tortola, Virgin Islands; Figures 339–341 a male from Tortola; Figure 342 from Isla Magdalena, Baja California; Figure 343 from Bocas del Toro, Panama. These specimens were chosen because there were several females collected with a male, and the male's abdominal shape (Fig. 339) resembles that of the female, supporting their determination. The female from Tortola (Fig. 335), where *C. berlandi* is uncommon, had a wider scape, and the posterior median area were smaller than in females from Mexico. The ventral white spots on the abdomen may be on tubercles. All females from Baja California had the abdomen shorter than in specimens from other regions. The specimens from Sierra Nevada de Santa Marta, Colombia (MNHN), have the posterior median area of the epigynum relatively small.

Diagnosis. The female differs from *C. bifurcata* by having six (Figs. 337, 338) rather than five abdominal tubercles, and it differs from *C. berlandi* and *C. pichilinque* by having the scape of the epigynum narrow, long, and with almost parallel sides (Figs. 333, 335). Only the three posterior abdominal tubercles separate the male *C. walckenaeri* (Fig. 339) from *C. turbinata*,

but some male *C. walckenaeri* may lack these tubercles. The keel on the median apophysis (Fig. 343) separates the male from *C. berlandi* (Fig. 332).

Natural History. Cyclosa walckenaeri has been found in diverse habitats: old coffee plantation; along fence at night; night collecting in Coamo; beach grapes in Puerto Rico; dwarf forest at El Yunque, Puerto Rico; citrus trees in the Lesser Antilles; savanna in Chiapas; thorn forest and on cactus in Baja California Sur; herbaceous vegetation and dry forest in northern Colombia.

Distribution. Florida and southern Texas to Colombia, West Indies to Guianas (Map 7A).

Specimens Examined. UNITED STATES *Florida*: *Collier Co.*: Naples, ♀ (AMNH). *Dade Co.*: Miami Beach, ♀ (MCZ). *Texas*: Edinburgh, ♀♂ (AMNH); 16 km SE Edinburg, ♀♂ (AMNH); 24 km SW Harlingen, ♀ (AMNH); 8 km E Rio Grande City (AMNH); Brownsville, ♀ (AMNH). MEXICO *Tamaulipas*: Las Calabazas, ♀ (USNM). *Baja California Sur*: Bahia de los Muertos, ♀♂ (CAS); 3 km E Cabo San Lucas, ♀ (CAS); Isla Magdalena, ♀♂ (CAS); ♀ (AMNH); 8 km S Miraflores Road to Las Casitas, ♀ (CAS); 8 km N La Paz, road to Pichilinque ♀ (CAS); La Paz, ♀ (CAS, MCZ); 63 km S La Paz on road to Todos Santos, ♀♂ (CAS); Punta Lobos, 1.6 km SE Todos Santos, ♀♂ (CAS); 4.8 km NW San Antonio, ♀ (CAS); 8 km W San José del Cabo, ♀♂ (DU); 11 km W San José del Cabo, ♀ (DU); 26 km NW Cabo San Lucas, ♀ (CAS); 25 km E San Lucas, ♀ (CAS); 19 km S Todos Santos, ♀ (CAS). *San Luis Potosí*: Tamazunchale, ♂ (AMNH). *Durango*: 16 km E El Salto, ♀ (AMNH). *Sinaloa*: 64 km S Culiacan, ♀ (AMNH); 8 km NW Río Culiacan, ♀ (AMNH). *Nayarit*: Tepic, ♀ (AMNH). *Veracruz*: Coscomatepec, ♀ (CAS); Jalapa, ♂ (CAS); 24 km W Jalapa, ♀ (AMNH). *México*: Toluca, ♀ (MCZ). *Michoácan*: 9.6 km N Cherán, ♂ (AD). *Puebla*: 6 km S Zacapoaxtla, 1♂ (AD). *Guerrero*: Tamarindos S. Papanoa, 17°17′N, 101°02′W, ♀ (MCZ). *Oaxaca*: Oaxaca, ♀ (MCZ); San Gerónimo, ♀ (AMNH); Soyaltepec, ♂ (AMNH). *Campeche*: Champoton, 19°21′N, 90°43′W, ♀ (MCZ); 6 km W Francisco Escarcega, ♂ (MCZ); outside Itacumbilxunan, S of Bolonchen de Rejon, Rt. 161, ♂ (MCZ). *Yucatan*: Chichen Itza, ♀♂ (AMNH); Balankanche Cave, 2 km E Chichen Itza, ♀ (MCZ); Dolores Otero, ♀ (AMNH); Uxmal, ♀ (CAS); 17.6 km E Valladolid on road to Ozal, 20°41′N, 88°10′W, 1♂ (CAS). *Quintana Roo*: Kohunlich ruins, 9 km S Francisco Villa, 18°26′N, 88°48′W, ♂ (MCZ). *Chiapas*: Cintalapa, ♀ (AMNH); El Real, ♀ (AMNH); Oaxaca, ♂ (AMNH); 24 km NW Arriaga, ♀ (AMNH); Lagunas de Montebello, ca. 48 km E Comitan, ♂ (CAS); 20 km NW Ocozocoautla, ♀ (CAS); La Zacualpa, ♂ (AMNH); Tapachula, ♂ (CAS). GUATEMALA Cobán, ♀ (AMNH). EL SALVADOR Instituto, ♀ (SMK). NICARAGUA Torreon, ♀ (JMM). COSTA RICA Chiral Paraiso [?], (MCZ); Gilarán [?], ♀ (MCZ). *San José*: Escazú, ♂ (USNM); San José, ♀ (AMNH). *Puntarenas*: Parrita, ♀ (MCZ). PANAMA *Bocas del Toro*: Río Changuinola, Corriente Grande, ♀♂ (MCZ). *Chiriquí*: Boquete, ♂ (MCZ); Cerro Punta, ♂ (AMNH). *Herrera*: 6 km Faldas Cerro Tigre, SE Paris, ♀ (MIUP); Sarigua, Dist. Parita, ♀♂ (MIUP). *Cocle*: Cerro Penã, nr. El Valle, ♀ (AMNH); Aguadulce, ♀ (AMNH). *Panamá*: La Chorrera, ♀ (AMNH); La Campana, 1♀ (AMNH); Univ. Panama campus, ♀ (AMNH).

BAHAMA ISLANDS *Berry Isl.*: Fraziers Hog Cay, ♂ (AMNH). *Cat Island*: Arthurs Town, ♀♂ (MCZ). *Great Abaco Isl.*: Marsh Harbor, ♂ (AMNH). *Long Island*: ♀ (MCZ). CUBA *Camagüay*: Camagüay, ♀ (AMNH); savannas, Agramonte Camagüay, ♀♂ (AMNH), Soledad, ♀♂ (MCZ). *Holguin*: Banes, ♀♂ (AMNH, MCZ). *Isla de Piños*: Sierra las Casas, ♀ (AMNH). *Matanzas*: Pan de Palenque, ♀ (AMNH). *Pinar del Río*: San Vicente, ♀♂ (AMNH). *Santa Clara*: Vega Alta, ♀ (AMNH). JAMAICA many records (AMNH, MCZ). HAITI Kenskoff, 1,400 m, ♀♂ (AMNH, MCZ); Port au Prince, ♀♂ (AMNH, MCZ); île de la Gonave, ♀ (AMNH). DOMINICAN REPUBLIC *La Altagracia*: Gran Chorra, ♀ (Del Monte Coll.); Playa Bayahiba, ♀ (MCZ). *Puerto Plata*: Puerto Plata, ♀ (MCZ). *Samana*: Sánchez, ♀ (AMNH). *Váldez*: W Beni, ♀ (AMNH). *Barahona*: Valle de Polo, ♂ (AMNH); Sierra Martín García, ♀ (AMNH). *La Vega*: Cordill. Central La Vega, ♀ (AMNH). PUERTO RICO very common, many records (AMNH, CAS, MCZ). VIRGIN ISLANDS *St. Croix*: Christiansted, ♀♂ (MCZ). *St. Thomas*: ♀ (AMNH, MCZ); Flagstik Hill, ♀ (AMNH). *St. John's*: ♀ (AMNH); Annaberg, ♀ (MCZ). BRITISH VIRGIN ISLANDS Little Saba, ♀ (AMNH); Peter Isl., ♀ (AMNH); Bath's and Devil's Bay, Virgin Gorda, ♀ (AMNH, MCZ); Salt Island, ♀ (AMNH); Tortola, ♀ (AMNH); Tortola, nr. Steele Point, ♀♂ (AMNH, MCZ). LESSER ANTILLES *Guadeloupe*: Marie Galante, ♀ (FSCA). TRINIDAD Bayshore, ♀ (AMNH).

VENEZUELA *Sucre*: Carúpano, ♀ (MNHN 18871). SURINAM Matappica Beach, ♀ (AMNH). COLOMBIA *Magdalena*: S Cabaña "Villa Culebra" nr. Bonda, ca. 10 km E Santa Marta, ♂ (SMK); Sierra Nevada de Santa Marta, ♀ (AMNH 8405); Gaira, ♀ (MCZ).

Cyclosa pichilinque new species
Figures 344–353; Map 7A

Holotype. Female holotype, male allotype and 14 female and three immature paratypes from Puerto de Pichilinque, Baja California Sur, Mexico, 22 Apr. 1944 (M. Correa), in AMNH, a female kept in

MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown, cephalic region yellowish (Fig. 346). Abdomen venter with black booklung covers and black spinnerets, and with a median white square that often includes a pair of black spots (Fig. 347). Abdomen with six tubercles (Fig. 346). Total length 4.0 mm. Carapace 1.6 mm long, 1.2 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.4 mm, patella and tibia 1.6, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.7, fourth 1.2. First femora shorter than corresponding patellae and tibiae, third and fourth slightly longer.

Male allotype. Coloration much darker than that of female, carapace brown. Abdomen with only three pairs of tubercles (Fig. 349). Total length 2.6 mm. Carapace 1.27 mm long, 1.14 wide in thoracic region, 0.48 wide behind posterior lateral eyes. First femur 1.27 mm, patella and tibia 1.27, metatarsus 0.63, tarsus 0.41. Second patella and tibia 1.04 mm, third 0.55, fourth 0.95.

Note. Males and females were collected together.

Variation. Specimens of *C. walckenaeri* from Baja California all have a slightly shorter abdomen than those from mainland Mexico and resemble *C. pichilinque.*

Diagnosis. Cyclosa pichilinque is distinguished from specimens of *C. walckenaeri* by having a short abdomen, barely longer than wide (Figs. 346–348), and by having the scape of the epigynum wider (Fig. 344) and the posterior median plate smaller (Fig. 345) than in *C. walckenaeri. Cyclosa pichilinque* is very distinct compared with mainland Mexican and West Indian specimens of *C. walckenaeri* but is less distinct from Baja California specimens.

Distribution. Baja California Sur (Map 7A); no other specimens were found.

Cyclosa serena new species
Figures 354–362; Map 6E

Cyclosa oculata:—Archer, 1963: 23. Erroneous determination.

Holotype. Female holotype, male allotype, one male and five female paratypes from Loma de Peñuelas, 6 km S de La Serena, Coquimbo Prov., Chile (A. F. Archer), in AMNH. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace dark brown, lightest on each side of cephalic region (Fig. 356). Abdomen venter with a pair of white patches. Abdomen with six tubercles (Figs. 356, 357). Total length 6.5 mm. Carapace 2.4 mm long, 1.5 wide in thoracic region, 0.8 wide behind posterior lateral eyes. First femur 2.0 mm, patella and tibia 2.5, metatarsus 1.2, tarsus 0.6. Second patella and tibia 2.0 mm, third 1.2, fourth 2.1. All femora shorter than corresponding patellae and tibiae.

Male allotype. Coloration as in female. Abdomen as in female, including all the tubercles (Fig. 359). Total length 4.6 mm. Carapace 2.0 mm long, 1.4 wide in thoracic region, 0.5 wide behind posterior lateral eyes. First femur 1.8 mm, patella and tibia 1.8, metatarsus 1.1, tarsus 0.6. Second patella and tibia 1.5 mm, third 0.4, fourth 1.5. Femur of first leg same length, others slightly longer than corresponding patellae and tibiae.

Males and females were collected together; *C. serena* appears to be the only species of *Cyclosa* in Chile.

Variation. Total length of females 5.1 to 8.3 mm, males 4.2 to 4.6. Argentinian specimens have only five tubercles, lacking the anterior median tubercle (Fig. 358). The illustrations were made from the female holotype and allotype, except Figure 358, which is from a specimen from Argentina.

Diagnosis. Cyclosa serena is distinguished from others by the short, parallel-sided scape of the epigynum (Fig. 354); the male has a unique anterior facing tooth on the margin of the median apophysis (Figs. 360, 362).

Natural History. One specimen came from a horizontal web between floating plants, in Santa Fé Province, Argentina.

Distribution. Argentina, Chile (Map. 6E).

Specimens Examined. ARGENTINA *Entre Ríos*: Nov. 1974, 1♂ (Cesari, MACN); *Córdoba*: Calamuchita, Mar. 1954, 1♀ (M. J. Viana, MACN); Mar. 1956, 1♂ (M. J. Viana, MACN). *Santa Fé*: Arroyo El Toba, 14 Oct. 1976, 1♀ (M. E. Galiano, MACN). CHILE *Atacama*: 3 km S Vallenar, 460 m, under stone, scrubby mountain side, 7 Jan. 1985, 1♀ (N. I. Platnick, O. F. Francke, AMNH). *Coquimbo*: Cerro de Talinay, Talinay, 29 Nov. 1961, 3♀ (A. F. Archer, AMNH); 32 km E La Serena, 3 Dec. 1950, 1♂ (E. S. Ross, A. E. Michelbacher, CAS). *Ñuble*: Chillán, 3♀ (L. Peña, IRSNB).

Cyclosa haiti new species
Figures 363–367; Map 3A

Holotype. Female holotype from La Visite, 6,000–7,000 ft [2,000–2,300 m], Haiti, 16–23 Sept. 1934 (P. J. Darlington), in MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Thoracic region of carapace dark brown grading into yellowish cephalic region (Fig. 365). Sternum mostly white with brown lines limiting white areas. Abdomen venter white with symmetrical dark lines (Fig. 366). Abdomen with a pair of anterior dorsal tubercles, a pair of posterior lateral tubercles and a single median, posterior tubercle (Figs. 465, 367). Total length 4.8 mm. Carapace 1.5 mm long, 1.0 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.4 mm, patella and tibia 1.6, metatarsus 0.8, tarsus 0.5. Second patella and tibia 1.4 mm, third 0.8, fourth 1.3. First and second femora shorter than corresponding patellae and tibiae, third and fourth of same length.

Variation. Total length of females 4.8 to 6.0 mm.

Diagnosis. Cyclosa haiti is distinguished from *C. walckenaeri* by having only five abdominal tubercles (Fig. 367) and from *C. bifurcata* by the narrower median plate in ventral and posterior views of the epigynum (Figs. 363, 364).

Distribution. Greater Antilles, Hispaniola, Jamaica and Haiti (Map 8A).

Specimens Examined. GREATER ANTILLES *Jamaica*: Portland Par., Hardwar Gap, 20 Nov. 1957, 1♀ (A. M. Chickering, MCZ). *Haiti*: Furcy, Mt. Cabaio, 2,100 m, 26 Mar. 1940, 1♀ (Folk, MCZ); Furcy, 1,600 m, 9 Jan. 1998, 2♀ (C. K. Starr, MCZ). *Mona Island*: Aug. 1944, 1♀ (H. Beatty, MCZ).

Cyclosa bifurcata (Walckenaer)
Figures 368–377; Map 8A

Epeira bifurcata Walckenaer, 1841: 145. Keyserling, 1864: 142, pl. 6, figs. 22, 23, ♀. Specimens from Guyana, lost. Keyserling, 1892: 97, pl. 5, fig. 72.

Epeira fusiformis Taczanowski, 1878: 173, pl. 2, fig. 22, ♀. Female lectotype here designated from hymenopteran nest, Amable María, Junín, Peru, in PAN, examined. The male paralectotype is an unknown *Wagneriana* species. NEW SYNONYMY.

Epeira walckenaerii Keyserling, 1892: 98, pl. 5, fig. 73, ♀, ♂. Paratypes only from Bogota, Colombia, Tacquara do Mundo Novo and Rio Grande do Sul, Brazil, in BMNH, examined. (Lost holotype and illustrations are *C. walckenaeri* Keyserling [=*walckenaeri* (O. P.-Cambridge)].)

Turckheimia scelesta O. P.-Cambridge, 1894: 268, pl. 39, fig. 10, ♀. Female holotype from San José, Costa Rica, in BMNH, examined. Erroneously synonymized with *C. diversa* by F. P.-Cambridge, 1904. NEW SYNONYMY.

Cyrtophora fusiformis:—Banks, 1898: 256.

Cyclosa fusiformis:—F. P.-Cambridge, 1904: 497. Roewer, 1942: 760. Bonnet, 1956: 1316.

Cyclosa globulifaciens Hingston, 1932: 90, 369. Female from Essequibo River, Guyana, in BMNH, lost. Roewer, 1942: 760. Bonnet, 1956: 1316. NEW SYNONYMY.

Cyclosa bifurcata:—Roewer, 1942: 759. Bonnet, 1956: 1309.

Note. I am following Keyserling's (1864) interpretation of *Epeira bifurcata* Walckenaer. Keyserling had specimens from Bogota that survived in the BMNH (1890.7.1.4639) and could be examined. In 1892 Keyserling redescribed *E. bifurcata*, and decided that some specimens of his are a second, similar species, because they have two median posterior tubercles on the abdomen, whereas *E. bifurcata* has only one. He named the new species *Epeira walckenaeri*, but some paratypes examined from Taquara do Mundo Novo [Rio Grande do Sul], Brazil, in the BMNH (1890.7.1.505/6), are also *bifurcata*, having a tiny, extra tubercle on the median posterior end of the abdomen. Keyserling's illustration is clearly *C. walckenaeri* (O. P.-Cambridge), recognized by the parallel margins of the scape of the epigynum. Keyserling's name *walckenaeri* is actually a

synonym, as well as a homonym, of *C. walckenaeri* (O. P.-Cambridge). Keyserling died in 1889 of tuberculosis of the brain (Bonnet, 1945) and his volume (1892) was published subsequently by G. Marx. Hingston (1932: 112, 113) mentions *C. bifurcata* and described *Cyclosa globulifaciens* with total length of 9 mm and with the characteristic abdominal tubercles of *C. bifurcata* (Walckenaer).

Cyclosa fusiformis was first placed in *Cyclosa* by F. P.-Cambridge.

The holotype of *Turckheimia scelesta*, marked *Cyclosa diversa*, arrived from the BMNH, but the label indicated that it was the type of *scelesta*.

Description. Female from Barro Colorado Island, Panama. Carapace dark brown grading into yellowish eye region (Fig. 370). Abdomen venter black with median black maculations and a pair of white patches (Fig. 371). Abdomen with only five tubercles (Figs. 370–372). Total length 8.0 mm. Carapace 2.8 mm long, 1.8 wide in thoracic region, 1.1 wide behind posterior lateral eyes. First femur 2.1 mm, patella and tibia 2.6, metatarsus 1.3, tarsus 0.7. Second patella and tibia 2.2 mm, third 1.3, fourth 2.3. All femora shorter than corresponding patellae and tibiae.

Male from Engo. Marcilac, São Paulo State, Brazil. Coloration much darker than in female; carapace brown (Fig. 373). Abdomen black, with a pair of anterior dorsal white patches (Fig. 373); venter with a pair of white spots. Sides with an irregularly shaped white longitudinal band. Abdomen with three posterior tubercles (Fig. 373). Total length 3.6 mm. Carapace 1.78 mm long, 1.35 wide in thoracic region, 0.49 wide behind posterior lateral eyes. First femur 1.49 mm, patella and tibia 1.45, metatarsus 0.86, tarsus 0.49. Second patella and tibia 1.18 mm, third 0.74, fourth 1.40. All femora about the same length as corresponding patella and tibia.

Note. Males and females are collected together infrequently.

Variation. Total length of females 5.3 to 9.7 mm, males 3.4 to 4.8. Some females show a minute tubercle in place of the missing dorsal one. The illustrations were made from a female from Barro Colorado Island, Panama, and a male from Engo. Marsilac, São Paulo, Brazil, collected with females. Most males are large and show the abdominal tubercles.

Diagnosis. Cyclosa bifurcata is distinguished from others by having only five abdominal tubercles (Figs. 370–372) and by having a very large median plate in the epigynum and the depressions close to the sides of the base (Fig. 368). The male palpus is very distinct, having the conductor projecting beyond the bulb and a long, curved conductor tooth (Figs. 374–376).

Natural History. Females were collected on sunny roadside in Trinidad, and on leaves of agave in Depto. Antioquia, Colombia; a male was collected by canopy fogging at the Tambopata Reserve in Peru and also as prey of sphecid wasps 80 km N of Manaus, Brazil.

Distribution. Widespread, from Hispaniola, Costa Rica, south to northern Argentina and southern Brazil (Map 8A).

Specimens Examined. COSTA RICA *San José*: San Antonio de Escazú, Feb. 1988, 2♂ (W. Eberhard, USNM). PANAMA *Cocle*: El Valle, Jan. 1947, 1♀ (N. L. H. Krauss, AMNH). *Panamá*: Barro Colorado Island, Aug. 1939, 1♀ (A. M. Chickering, MCZ); Sept. 3♀ (P. Rau, MCZ); Summit, Nov. 1946, 1♀ (N. L. H. Krauss, AMNH).

GREATER ANTILLES *Hispaniola*: Dominican Republic, Puerto Plata, July, Aug. 1941, 8♀ (D. Hurst, MCZ). LESSER ANTILLES *Trinidad*: El Tucuche, 16 Dec. 1934, 3♀ (N. A. Weber, MCZ); Simla, 25 Apr. 1964, 2♀ (A. M. Chickering, MCZ); La Laja Road, Arima Parish, 7 Feb. 1984, 1♀ (J. Coddington, USNM).

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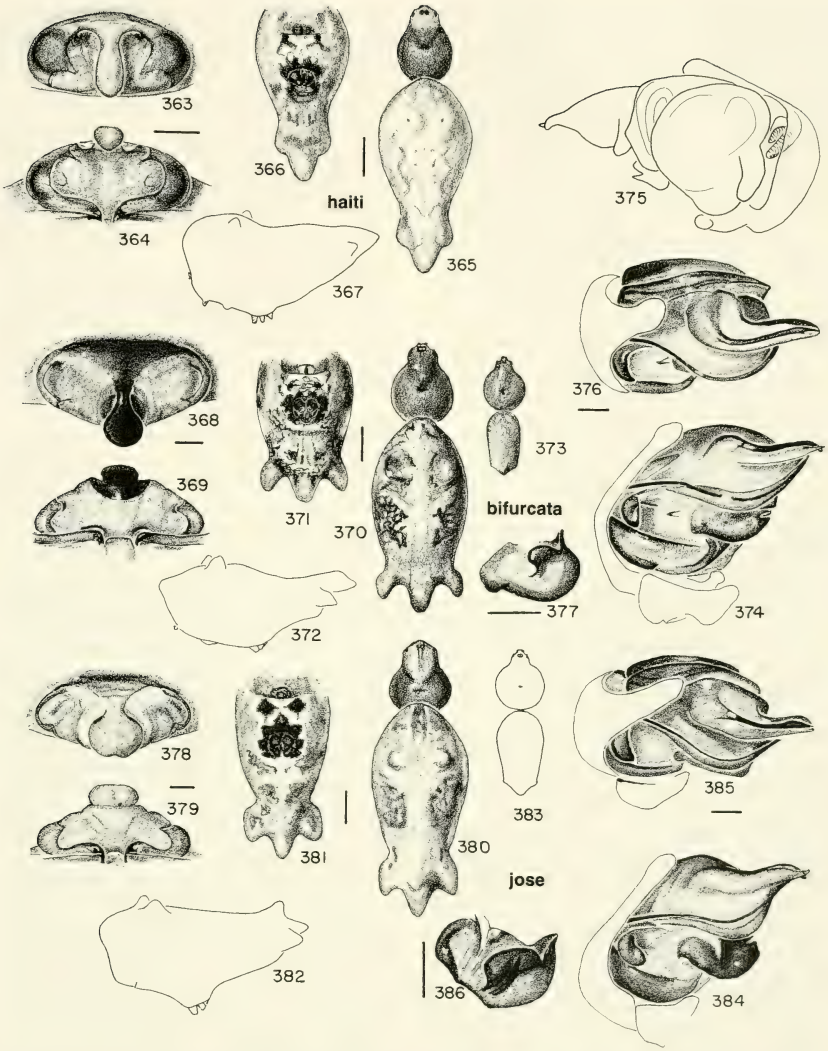
Figures 363–367. *Cyclosa haiti* n. sp., female. 363, 364, epigynum. 363, ventral. 364, posterior. 365, dorsal. 366, abdomen, ventral. 367, abdomen, lateral.



Figures 368–377. *C. bifurcata* (Walckenaer). 368–372, female. 368, 369, epigynum. 368, ventral. 369, posterior. 370, dorsal. 371, abdomen, ventral. 372, abdomen, lateral. 373–377, male. 373, dorsal. 374–377, left palpus. 374, mesal. 375, dorsal. 376, apical. 377, median apophysis.

Figures 378–386. *C. jose* n. sp. 378–382, female. 378, 379, epigynum. 378, ventral. 379, posterior. 380, dorsal. 381, abdomen, ventral. 382, abdomen, lateral. 383–386, male. 383, dorsal. 384–386, palpus. 384, mesal. 385, apical. 386, median apophysis.

Scale lines: 1.0 mm; genitalia 0.1 mm.

GUYANA Kartabo, 1924, 1♀ (AMNH). SURINAM *Brokopondo*: Browns Berg, 5°N, 55°27′W, 20 Feb. 1982, 1♀ (D. Smith Trail, MCZ). FRENCH GUIANA Isles de Salut, 1♂ (K. Jelski, PAN). VENEZUELA *Aragua*: Rancho Grande, 1♀ (C. T. Collins, AMNH). COLOMBIA *Magdalena*: Sierra Nevada de Santa Marta, 1♀ (MNHN 8405a). *Santander*: Río Suárez, 800–1,000 m, 11–17 Aug. 1946, 1♀ (AMNH). *Antioquia*: El Peñol, 2,100 m, 9 Mar. 1974, 1♀ (A. B. Schneble, MCZ); San Vicente, 29, 30. Dec. 1986, 3♀ (M. A. Serna, MCZ). *Cundinamarca*: along dirt road 3 mi SE Finca Bella Vista, W Sosaima, 13 May 1965, 1♀ (P. R., D. L. Craig, CAS). *Boyacá*: Río Upia, 800–950 m, Nov., Dec. 1945, 1♀ (AMNH). *Huila*: Finca Meremberg, 10 km E Sta. Leticia, Mar. 1979, 3♀, 2♂ (W. Eberhard 1867, MCZ); 12 km W Sta. Leticia, 2,300 m, Mar. 1976, 1♂ (W. Eberhard, 1077, MCZ); 12 km E Sta. Leticia, 2,300 m, Mar. 1976, 3♀, 1♂ (W. Eberhard 1078, MCZ). *Putumayo*: El Pepino, 1,000 m, on road to Mocoa, 21 May 1973, 1♀ (N. Leist, SMNK). ECUADOR *Napo*: Coca, 9–19 Feb. 1986, 1♀ (McKamey, DU); 20 km E Puerto Napo, Alinahui, 01°00′S, 77°25′W, Oct. 1945, 4♀ (V., B. Roth, CAS). *Morena-Santiago*: Chiguaza, Wakani Prov., 22 May 1977, 2♀ (N. Engler, MCZ). PERU *Loreto*: Pebas (& São Paulo de Olivença), 1♂ (M. de Mathan, MNHN 4095a). *Cuzco*: Quincemil [Río Marcapata], 750 m, 13 Apr. 1947, 1♀ (J. C. Pallister, AMNH). *Madre de Dios*: Zona Reservada Tambopata, 14 June 1988, 1♀ (J. Coddington, MUSM); 6–14 Sept. 1984, 1♂ (T. L. Erwin, USNM). *Ayacucho*: Moyobamba, 2♀ (M. de Mathan, MNHN 10574). BRAZIL *Pará*: Canindé, Rio Gurupi, Mar–May 1964, 1♀, 1 imm. (J. Carvalho, AMNH). *Amazonas*: Km 41 Reserve, 60 km N Manaus, 18 Apr. 1991, 1♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ); 80 km N Manaus, areas of Smithsonian, 1988–90, 1♂ (E. Morato, SMNK); Manaus, Reserva Ducke, 1 July 1987, 1 imm. (H. Höfer, SMNK); Manaus, Igapó Tarumã Mirím, 25 Sept. 1987, 1♀ (H. Höfer, SMNK). *Alagoas*: Manguburas, Camargo, Andrade, Oct. 1952, 1♀ (A. Dente, MZSP 13154). *Bahia*: Fazenda Almada, Uruçuca, 27 Nov. 1977, 2♂ (J. S. Santos, MCN 10343, 10491a); Iguaçu, 1 Aug. 1924, 1♀ (A. Roman, NHRM). *Mato Grosso*: Barro do Tapirapé, 5–10 Feb. 1964, 1♀ (B. Malkin, MZSP 3347). *São Paulo*: Campos da Serra, ca. Ribeira do R Magi Grassú, 3 Apr. 1943, 1♂ (F. Lane, MZSP 13 158); Estr. Santo Amaro, Eng Marcilac, 29 June 1966, 10♀, 1♂ (P. Biasi, MZSP 1948); Eng. Marcilac, 30 June 1967, 1♀ (P. Biasi, MZSP 6943); Ipiranga, 9 Mar. 1948, 1♂ (P. Caneschi, MZSP 10779). *Paraná*: Corupa, Feb. 1949, 1♀ (A. Maller, AMNH); Foz de Iguaçu, 18 Oct. 1995, 1♀ (H. Höfer, SMNK); Rio Azul, 3 Apr. 1993, 1♀ (R. Bóçon, MCN 23606). *Rio Grande do Sul*: Caçapava do Sul, 24 July 1977, 1♀ (D. Link, MCN 6326); Campo Bom, 19 Oct. 1987, 1♀ (C. J. Becker, MCP 0127); Capaneumho, Cachoeira do Sul, 12 May 1993, 1♀ (R. G. Buss, MCP 3612); Gravataí, 2 Feb. 1992, 1♂ (A. D. Brescovit MCN 22101); Montenegro, 3 Nov. 1977, 1♂ (A. A. Lise, 7150); Santa Maria, 8 Oct. 1985, 2♀ (I. M. Dall' Astra, MCN 15286); São Leopoldo, 1 May 1964, 1♀ (C. Valle, MZSP 6955); Tenente Portela, 29 Nov. 1978, 1♂, 1 imm. (H. Bischoff, MCN 3489, 8427a); Viamão, 23 June 1991, 1♀ (L. Moura, MCN 21202). PARAGUAY *Alto Paraná*: Tatiyupi Reserve, 14 June 1984, 1♀ (L. Baert, J. P. Maelfait, IRSNB). ARGENTINA *Misiones*: Cataratas de Iguazú, 26 Mar. 1968, 1♀ (M. E. Galiano, MACN); Mar. 1976, 1♀, 1♂ (R. M. Capocasale, CAS); Eldorado, 26°28′S, 54°43′W, Sept.–Nov. 1964, 1♀ (A. Kovacs, AMNH); Montecarlo, 5 Dec. 1965, 1♀ (Giacchi, AMNH); Pto. 17 de Octubre, Oct. 1954 [Puerto Libertad], 1♀, 2♂ (R. D. Schiapelli, de Carlo, MACN); Pto. Bemberg [Puerto Libertad], Oct.–Dec. 1952, 1♂ (M. J. Viana, MACN 3586); 1 May 1953, 1♀ (A. Giai, W. Partridge, MACN 3136); Sept. 1963, 5♀ (R. D. Schiapelli, de Carlo, MACN); Río Urugua-í, Sept. 1948, 1♀, 1♂ (A. Giai, MACN 5516); Santa María, Dec. 1948, 1♀ (M. J. Viana, MACN); Nov., Dec. 1952, 1♀, 1♂ (M. J. Viana, MACN 3585).

Cyclosa jose new species
Figures 378–386; Map 8B

Holotype. Female holotype and male paratype from nr. San José, San José Prov., Costa Rica, 1,100 m, Aug. 1979 (W. Eberhard, 1882–91), in MCZ. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace beige, sides of thorax dark brown (Fig. 380). Abdomen venter with three black patches (Fig. 381). Abdomen with a dorsal pair of humps and four posterior tubercles (Figs. 380–382). Total length 8.5 mm. Carapace 2.5 mm long, 1.9 wide in thoracic region, 1.0 wide behind posterior lateral eyes. First femur 1.9 mm, patella and tibia 2.4, metatarsus 1.2, tarsus 0.6. Second patella and tibia 2.0 mm, third 1.2, fourth 2.1. All femora shorter than corresponding patellae and tibiae.

Male paratype. Coloration darker than in female, carapace brown. Abdomen with small pair of anterior and three posterior tubercles (Fig. 383). Total length 4.6 mm. Carapace 2.0 mm long, 1.5 wide in thoracic region, 0.6 wide behind posterior lateral eyes. First femur 1.7 mm, patella and tibia 1.6, metatarsus 0.9, tarsus 0.5. Second patella and tibia 1.3 mm, third 0.8, fourth 1.4. All femora about same length as corresponding patellae and tibiae.

Note. Males and females were collected together.

Diagnosis. *Cyclosa jose* is distinguished from *C. bifurcata* by having six tubercles on the abdomen (Figs. 380–382) and by having a short, nearly circular scape (Fig. 378). The lobe of the median apophysis of the male palpus is wider (Fig. 386) than that of *C. bifurcata* (Fig. 377).

Distribution. Costa Rica (Map 8B).

Specimens Examined. COSTA RICA *San José*: San José, zoological park, 7 Jan. 1979, 1♂ (J. Coddington, MCZ).

Cyclosa vicente new species
Figures 387–390; Map 6E

Holotype. Female holotype from São Vicente do Sul, Rio Grande do Sul, Brazil, 2 Dec. 1981 (C. J. Becker), in MCN no. 9936. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace yellow with white setae, sides of thoracic region brown (Fig. 389). Abdomen white with some gray streaks dorsally (Fig. 389); venter white. Abdomen with two pairs of dorsal tubercles, two median posterior, and one pair between epigynum and spinnerets (Figs. 389, 390). Total length 6.0 mm. Carapace 2.1 mm long, 1.5 wide in thoracic region, 0.9 wide behind posterior lateral eyes. First femur 1.6 mm, patella and tibia 1.9, metatarsus 1.0, tarsus 0.5. Second patella and tibia 1.7 mm, third 1.1, fourth 1.8. All femora shorter than corresponding patellae and tibiae.

Note. *Cyclosa espumoso* may be the male of *C. vicente*.

Variation. Total length of females 5.7 to 6.7 mm.

Diagnosis. Unlike *C. diversa*, *C. vicente* has the seminal receptacles placed more anteriorly (Fig. 387), and there is a pair of deep notches on the posterior median plate (at 2h and 10h in Fig. 388).

Specimens Examined. BRAZIL *Mato Grosso*: Chavantina, Oct. 1946, 1♀ (H. Sick, MZSP 1319). *São Paulo*: Piracununga, 13 June 1950, 1♀ (Schubart, MZSP 7117). *Paraná*: Cavinna [?], 1947, 1♀ (A. Maller, AMNH); Rolândia, 1948, 1♀ (A. Maller, AMNH). *Santa Catarina*: Corupá, Feb. 1949, 1♀ (A. Maller, AMNH). *Rio Grande do Sul*: 1♀ (P. Rambo, MNRJ); Guaíba, 29 Oct. 1994, 1♀ (A. A. Lise, MCP 5655); Viamão, 19 Apr. 1996, 1♀ (A. A. Lise, MCN 0632a). ARGENTINA *Misiones*: Puerto Bemberg [Puerto Libertad], Pasarela del Río Urugua-í, Jan, Feb. 1950, 1♀ (A. Giai, W. Partridge, MACN 3137).

Cyclosa diversa (O. P.-Cambridge)
Figures 391–412; Map 8B

Turckheimia diversa O. P.-Cambridge, 1894: 136, pl. 16, fig. 11, ♀. Female lectotype here designated, and three female and one immature paralectotypes from Teapa, Tabasco, Mexico, in BMNH, no. 1905.4.28.2888–93, examined.

Cyclosa diversa:—F. P.-Cambridge, 1904: 496, pl. 47, fig. 10, ♀. Roewer, 1942: 759. Bonnet, 1956: 1316. Alayón, 1993: 4, fig. 3, ♀.

Cyclosa brevis Bryant, 1940: 335, fig. 110, ♂. Male holotype from Soledad garden, Cienfuegos Prov., Cuba, in MCZ, examined. Brignoli, 1983: 266. Alayón, 1993: 2. NEW SYNONYMY.

Cyclosa nodosa:—Alayón, 1982: 4 [not *nodosa* (O.P.-Cambridge].

Note. The *Turckheimia diversa* type material, including five specimens, was labeled *Cyclosa diversa* (O. P. Cambr.). One with a broken embolus on the left side in the epigynum was designated lectotype; of the other four, one had a broken embolus on its right side, one female lacked the embolus, the third had an unsclerotized epigynum (apparently it had just molted), and the fourth was immature.

The female, erroneously described by Alayón for *Cyclosa brevis*, is an unnamed species of *Wagneriana*.

Description. Female from Chiapas. Thoracic region of carapace brown, grading into yellowish cephalic region (Fig. 401). Abdomen venter black with a pair of white patches (Fig. 405). Abdomen with an anterior pair of tubercles, a posterior pair and two median posterior tubercles (Figs. 401–404). Total length 6.5 mm. Carapace 2.4 mm long, 1.8 wide in thoracic region, 1.1 wide behind posterior lateral eyes. First femur 1.7 mm, patella and tibia 2.2, metatarsus 1.0, tarsus 0.6. Second patella and tibia 1.6 mm, third 1.1, fourth 2.0. Femora shorter than corresponding patellae and tibiae except third, which is of same length.

Male holotype of *C. brevis*. Carapace dark brown grading into yellowish cephalic region (Fig. 406). Sternum brown. Abdo-

men white with black marks (Fig. 406); venter black with a pair of white spots. Abdomen with four indistinct tubercles, only posterior median one distinct (Fig. 406). Total length 2.4 mm. Carapace 1.26 mm long, 1.00 wide in thoracic region, 0.44 wide behind posterior lateral eyes. First femur 0.79 mm, patella and tibia 0.98, metatarsus 0.49, tarsus 0.35. Second patella and tibia 0.78 mm, third 0.48, fourth 0.74. Femora shorter than corresponding patellae and tibiae except third, which is slightly longer.

Note. Males and females were not collected together. They are matched because of the long tooth of the male palpal conductor, which breaks off and remains stuck in the female epigynum (Figs. 393, 395, 399).

Variation. Total length of females 4.3 to 11.5 mm, males 2.0 to 4.3. This species is variable. The abdomen may have the posterior median tubercles swollen (Figs. 402, 403), the length of the epigynal scape varies (Figs. 391, 397), the shape of the median plates is variable (Figs. 391–400). At first, I considered *C. diversa* to be numerous similar species but later could not separate them anymore. Figures 391 and 392 illustrate specimens from Oaxaca, Mexico; Figures 393, 394, 402 from Honduras; Figures 395, 396 from Costa Rica; Figures 397, 398 from Depto. Valle, Colombia; Figures 399, 400, 404 from Manaus, Brazil; Figure 401 from Chiapas, Mexico; and Figures 403, 405 from Rio Grande do Sul. Figures 406, 411, 412 illustrate males from Manaus, Brazil; Figures 407, 408 from Veracruz, Mexico; and Figures 409, 410 from Cuba.

Diagnosis. The female *C. diversa* may be distinguished from other *Cyclosa* species by the swollen posterior lateral tubercles frequently found on the abdomen (Figs. 402, 403), but not always present. Also, it can be distinguished by the club-shaped scape with depressions next to the base of the scape (Figs. 391, 393, 395, 397, 399), by the broken conductor teeth remaining in the epigynum and by the openings of the epigynum, best seen in posterior view, which are always separated from the lateral margin by about one-quarter of the width of the base (Figs. 392, 394, 396, 398, 400). The male can be separated from other species by the long conductor tooth (Figs. 407–410), which is frequently broken off (Figs. 411, 412). Unlike *C. bifurcata*, (Figs. 374–376), in *C. diversa* the conductor does not project beyond the bulb (Figs. 407, 408).

Natural History. A female was collected in cloud forest in Colombia, and by fogging canopy in Tambopata Reservation, Peru. *Cyclosa diversa* uses golden instead of white silk (W. Eberhard, personal communication)

Distribution. Widespread, Mexico to Argentina and Greater Antilles (Map 8B).

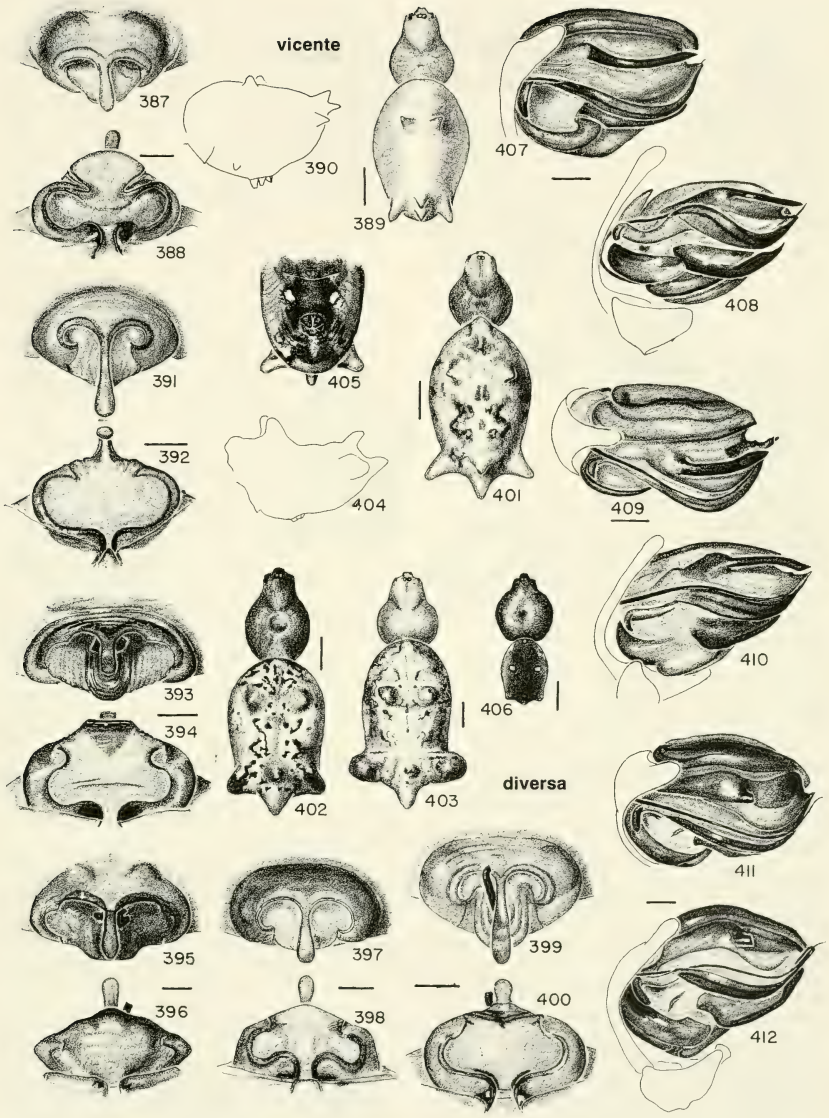
Specimens Examined. MEXICO San Rafael [?], 1♂ (N. Banks, MCZ). *San Luis Potosí*: 6.4 km E bridge, Río Axtla, 8 Jan. 1952, 1♀ (W. S. Creighton, AMNH). *Veracruz*: Córdoba, 21 Sept. 1984, 1♂ (C. W. Melton, C Agnew, AD); Fortín, 25 July 1956, 1♂ (V. Roth, W. J. Gertsch, AMNH). *Oaxaca*: Palomares, 12 Aug. 1963, 1♀ (D. Bixler, MCZ). *Chiapas*: La Zacualpa, Aug. 1909, 1♀ (A. Petrunkevitch, AMNH). GUATEMALA Quezaltenango, Dec. 1947, 1♀ (H. Wegener, AMNH). EL SALVADOR Santa Tecla, 8 Oct. 1949, 1♀ (J. Boursot, AMNH). HONDURAS *Atlántida*: Lancetilla, 18 July 1929, 1♀ (A. M. Chickering, MCZ). COSTA RICA *Heredia*: La Selva, nr. Puerto Viejo, 100 m, Mar. 1983, 1♀ (W. Eberhard SAE 23, TL 53-8, MCZ); 14 Jan. 1984, 1♀ (W. Eberhard 2319, MCZ).

CUBA *Habana*: Habana, NE San Antonio Baños

→

Figures 387–390. *Cyclosa vicente* n. sp., female. 387, 388, epigynum. 387, ventral. 388, posterior. 389, dorsal. 390, abdomen, lateral.

Figures 391–412. *C. diversa* (O. P.-Cambridge). 391–405, female. 391–400, epigynum. 391, 393, 395, 397, 399, ventral. 392, 394, 396, 398, 400, posterior. 391, 392, (Oaxaca, Mexico). 393, 394, (Honduras). 395, 396, (Costa Rica). 397, 398, (Depto. Valle, Colombia). 399, 400, (Manaus, Brazil). 401–403, dorsal. 401, (Chiapas, Mexico). 402, (Honduras). 403, (Rio Grande do Sul, Brazil). 404, abdomen, lateral. 405, abdomen, ventral (Rio Grande do Sul, Brazil). 406–412, male. 406, dorsal. 407–412,



left palpi. 407, 409, 411, apical. 408, 410, 412, mesal. 407, 408, (Veracruz, Mexico). 409, 410, (Cuba). 411, 412, (Manaus, Brazil).

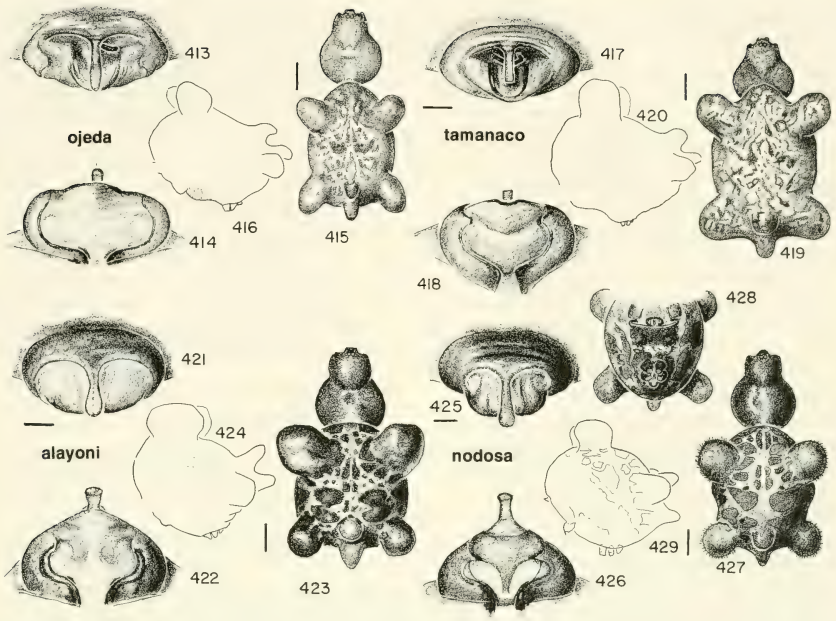
Scale lines: 1.0 mm; genitalia 0.1 mm.

nr. Nico, July 1978, 1♀ (G. Alayon, MCZ). TRINIDAD Simla, 6.4 km N Arima, 10 May 1981, 1♀ (R. West, MCZ).

VENEZUELA *Monagas*: Caripito, 1 July 1942, 1♀ (W. Beebe et al., AMNH). *Mérida*: road to Mérida nr. La Azulita, 10 Dec. 1977, 1♀ (Y. Lubin, MCZ). COLOMBIA *Magdalena*: Gaira, 10 m, Dec. 1975 (W. Eberhard, MCZ). *Cundinamarca*: Silvania, 1,500 m, 11 Oct. 1987, 1♀ (C. Valderrama, MCZ). *Meta*: Carimagua, Oct 1973, 1♀ (W. Eberhard, MCZ); 5 km W Villavicensio, 920 m, 2 Mar. 1955, 1♀ (E. I. Schlinger, E. S. Ross, CAS); Lomalinda nr. Puerto Lleras, 03°18′N, 73°22′W, 300 m, Aug. 1998, 1♀ (B. T. Carroll, V., B. Roth, CAS). *Valle*: Atumcela, 800 m, 15 Dec. 1969, 1♀ (W. Eberhard, MCZ); Centro Exper. de Hoechst Colombiana, Palmira, 7 Sept. 1991, 1♀ (H. Bastidas, MCZ), nr. Cali, Oct. 1973, 1♀ (W. Eberhard 639, MCZ); 1975, 1♀ (W. Eberhard 1141, MCZ); Lago Calima, 1,400 m, Jan. 1979, 1♂ (W. Eberhard 1822, MCZ); Río Jamundi, 1,000 m, 1972, 1♀ (W. Eberhard 524, MCZ); nr. Queremal, 1,600 m, Aug. 1977, 2♀ (W. Eberhard, MCZ); Santander, 1,000 m, 13 Mar. 1970, 1♀ (W. Eberhard, MCZ). *Cauca*: betw. Prendamo and Mondomó, 1♀ (W. Eberhard, MCZ). *Vaupés*: Abijya, 00°62′N, 69°59′W, 19 Mar. 1988, 1♂ (B. T. Carroll, CAS). *Nariño*: Reserva Natural la Planada, Ricaurte, 01°09′N, 77°58′W, 2♀ (C. Valderrama, CV); Chachaqül, nr. airport, 19 Aug. 1973, 1♀ (N. List, SMNK). ECUADOR *Sucumbíos*: Cuyabeno, Tarapoa, 23 June–1 July 1988, 1♀ (W. Maddison, MCZ); Río Tarapoa, 28 Apr. 1984, 1♀ (L. Avilés, MECN). *Cotopaxi*: Río Palenque, Nov. 1977, 1♂ (T. deVries, MECN). *Pastaza*: Puyo, 18 Apr. 1958, 1♂ (R. W. Hodges, MCZ). PERU *Loreto*: Río Samiria, 10 May–24 June 1990, 6♀ (T. Erwin, D. Silva, MUSM). *Huánuco*: Ayacu, 1 June 1967, 1♀ (A. F. Archer, AMNH); Tingo María, 2 June 1967, 1♀ (A. F. Archer, S. Risco, AMNH); Monson Valley, Tingo María, 19 Oct. 1954, 2♀; 10 Nov. 1954, 1♀; 2 Dec. 1954, 1♀ (E. I. Schlinger, E. S. Ross, CAS); Boqueron del Padre Abad, 28 Dec. 1986, 1♀ (D. Silva, MUSM). *Junín*: Estancia Naranjal, San Ramón, 20–27 July 1965, 1♀ (P. Wygodzinsky et al., AMNH). *Madre de Dios*: Zona Reservada, Parque Nacional Manu, Pakitza, 10–19 Oct. 1991, 2♀, 1♂ (D. Silva, USNM); Zona Reservada Tambopata, 2–10 May 1984, 1♀ (T. L. Erwin, USNM); 6–14 Sept. 1984, 1♀; 23 July 1987, 1♀ (D. Silva, MUSM); 15 km Puerto Maldonado, 28 July 1989, 2♀ (D. Silva, MUSM). *Cuzco*: Quincemil, 13 Aug. 1947, 1♀ (J. C. Pallister, CAS). *Arequipa*: Pooquerón, 470 m, Aug. 1946, 1♀ (F. Woytowski, AMNH). BRAZIL *Pará*: Belém, Fazenda Velha, Aug. 1970, 1♀ (M. Galiano, MACN). *Amazonas*: Reserva Km 41, 80 km N Manaus, 17 Apr. 1991, 1♀ (H. Fowler, E. Venticinque, R. S. Vieira, MCZ); Reserva Ducke, Manaus, 1♂ (A. A. Lise, MCP 2026); 15–23 Aug. 1991, 1♀ (A. Brescovit, MCN 21409); 6–9 Aug. 1992, 1♀ (A. D. Brescovit, MCN 22311). *Minas Gerais*: Lavras, 1 Mar. 1979, 1♂ (W. D. Fronk, MCZ). *Espírito Santo*: Rio São José, 26 Sept. 1942, 1♀ (B. Soares, MZSP 13159); Santa Leopoldina, 28 Aug. 1942, 4♀ (B. Soares, MZSP 8428). *Rio de Janeiro*: Rio de Janeiro, 1♀ (MNRJ 366); 1♀ (Thayer Exped., MCZ); Pinheira, Rio de Janeiro, 2♀ (MNRJ 369); Jardim Botânico, 19 Sept. 1990, 1♀ (H. Höfer, INPA). *São Paulo*: Barueri, 26 June 1966, 1♂ (K. Lenko, MZSP 5912); Capital, 15 July 1941, 1♂ (J. Damigo, MZSP 13151); Guarulhos, 14, 15 June 1942, 7♀ (P. Pereira, MZSP 5206, 8427); June 1947, 6♀ (P. Pereira, MZSP 4615); 5 July 1942, 1♀ (P. Pereira, MZSP 7281); Instituto Botânico, 18 Aug. 1967, 1♀ (P. Biasi, MZSP 6545); Ipiranga Cap, 12 June 1948, 2♀ (F. Lane, MZSP 7327, 7355); Registro Microbacia, R. Quilombo, 16 Apr. 1990, 1♂ (P. Gnaspini, MZSP 11857); Ribeirão Pires, Cid. São Paulo, 700–800 m. Dec. 1945, 1♀ (H. Sick, AMNH). *Paraná*: Refúgio Biólogico de Santa Helena, Santa Helena, 12–16 Nov. 1991, 1♂ (A. B. Bonaldo, MCN 21828). *Santa Catarina*: Morro do Baúilhota, 13 May 1996, 1♀ (C. N. Duckett, MCN 27561); Rio Vermelho, Mar. 1951, 1♀ (R. von Diringshofen, MZSP 13219). *Rio Grande do Sul*: Alto Casemiros, Cachoeira do Sul, 26 Sept. 1992, 1♂ (R., G. Buss, MCP 3468); Encantado, 21 Sept. 1985, 1♂ (A. D. Brescovit, MCN 14497); Itaúba, Arroio do Tigre, 15 Apr. 1978, 1♀ (A. A. Lise, MCN 7955); Novo Hamburgo, Morro dos Bois, Lomba Grande, 27 Nov. 1980, 1♂ (A. A. Lise, MCN 9416); Porto Alegrem Morro do Côco, 25 Apr. 1975, 1♂ (A. A. Lise, MCN 10515); Santa Maria, 2 Nov. 1985, 1♂ (A. D. Brescovit, MCN 14599); 1♀ (T. White, MCZ); São Leopoldo, 20 Sept. 1965, 1♀ (S. Valle, MZSP 5494); Viamão, 19 Aug. 1994, 1♀ (A. Braul, MCP 7712). BOLIVIA *La Paz*: Apolo, 1,400 m, 5–15 Aug. 1989, 1♀ (L. E. Peña, AMNH); Inquisivi, 2,300 m, 5, 6 Dec. 1984, 1♀ (L. Peña, AMNH). PARAGUAY Asunçion, Bolivia [probably an error of local.], 3♀ (MNHN 6519). *Alto Paraná*: Itala Reserve, 19 June 1984, 1♂ (L. Baert, J. P. Maelfait, IRSNB). *San Pedro*: San Estanislao, Sept. 1946, 2♀ (W. Hanke, MACN 1778, 1791). ARGENTINA *Misiones*: Eldorado, Sept.–Nov. 1964, 1♂ (A. Kovacs, AMNH); Santa María. Oct. 1944, 1♀ (M. J. Viana, MACN 1544); Puerto 17 de Octubre [Puerto Libertad], Oct. 1953, 1♂ (R. D. Schiapelli et al., MACN 3905); 4♀ (De Carlo et al., MACN 3887). *Salta*: Santa María, July 1957, 1♀ (A. G. Giai, MACN 2241). *Santa Fé*: Las Gamas, 20 km W Vera, 27–30 Oct. 1994, 2♀ (M. Ramires, J. Faibovich, MACN). *Entre Ríos*: Gualeguay, 26 Mar. 1943, 1♀ (H. Rossi, MACN, 1560). *Río Negro*: El Bolsón area, 1965, 1966, 1♀ (A. Kovacs, AMNH).

Cyclosa ojeda new species
Figures 413–416; Map 6F

Holotype. Female holotype from Curaçao, Netherland Antilles, no date, and an exclamation mark, in the MNHN no. 4303. The specific name is a noun in apposition after Alfonso de Ojeda, the discoverer of the island.



Figures 413–416. *Cyclosa ojeda* n. sp., female. 413, 414, epigynum. 413, ventral. 414, posterior. 415, dorsal. 416, abdomen, lateral.

Figures 417–420. *C. tamanaco* n. sp., female. 417, 418, epigynum. 417, ventral. 418, posterior. 419, dorsal. 420, abdomen, lateral.

Figures 421–424. *C. alayoni* n. sp., female. 421, 422, epigynum. 421, ventral. 422, posterior. 423, dorsal. 424, abdomen, lateral.

Figures 425–429. *Cyclosa nodosa* (O. P.-Cambridge), female. 425, 426, epigynum. 425, ventral. 426, posterior. 427, dorsal. 428, abdomen, ventral. 429, abdomen, lateral.

Scale lines: 1.0 mm; genitalia 0.1 mm.

Note. The exclamation mark on the original label indicates that the collector was E. Simon.

Description. Female holotype. Carapace dark brown, a yellowish patch on each side of cephalic region (Fig. 415). Venter of abdomen black with a distinct pair of white spots. Abdomen with six tubercles, four spherical and a cylindrical median pair (Figs. 415, 416). Total length 7.7 mm. Carapace 2.8 mm long, 2.2 wide in thoracic region, 1.2 wide behind posterior lateral eyes. First femur 2.1 mm, patella and tibia 2.5, metatarsus 1.3, tarsus 1.1. Second patella and tibia 2.2 mm, third 1.0, fourth 2.2. Femora shorter than corresponding patellae and tibiae. First and second tibiae curved.

Diagnosis. The abdomen is blackish brown with a distinct pattern of dark lines and dots (Fig. 415). *Cyclosa ojeda* is distinguished from *C. tamanaco*, which has a similar abdomen, by the wide posterior median plate of the epigynum (Fig. 414).

Distribution. Curaçao (Map 6F); no other specimens were found.

Cyclosa tamanaco new species
Figures 417–420; Map 6F

Holotype. Female holotype from Trinidad, Lesser Antilles, 17 July 1899 (J. H. Hart), in USNM. The specific name is a noun in apposition after the Carib tribe who were the original inhabitants of the island.

Description. Female holotype. Carapace dark brown with indistinct net-shaped pattern (Fig. 419). Abdomen brown with lines and dots (Fig. 419), venter dark without white patches. Abdomen with six spherical tubercles (Fig. 419). Total length 7.8 mm. Carapace 2.9 mm long, 2.1 wide in thoracic region, 1.3 wide behind posterior lateral eyes. First femur 2.0 mm, patella and tibia 2.4, metatarsus 1.2, tarsus 0.7. Second patella and tibia 2.2 mm, third 1.4, fourth 2.3. Length of femora shorter than adjacent patellae and tibiae. First and second tibiae curved.

Diagnosis. *Cyclosa tamanaco* differs from *C. nodosa* by the streaked marking of the abdomen and is distinguished from *C. ojeda* by having the posterior median plate smaller, and the openings of the epigynum closer together (Fig. 418).

Distribution. Trinidad (Map 6F), no other specimens were collected.

Cyclosa alayoni new species
Figures 421–424; Map 6F

Cyclosa nodosa:—Alayón, 1982: 4 [not *C. nodosa* (O. P.-Cambridge)].

Holotype. Female holotype from NE of San Antonio de los Baños, Habana, Cuba (G. Alayón), in MNHNC. The species has been named after the collector, Cuban arachnologist, Giraldo Alayón.

Description. Female holotype. Carapace, chelicerae, labium, endites dark brown. Sternum dark brown with a white median line that spreads anteriorly. Abdomen brown with trapezoidal, oval or round dark patches that are slightly sclerotized (Fig. 423), venter dark without white patches. Abdomen with two pairs of spherical, dorsal tubercles and two median posterior cylindrical tubercles (Figs. 423, 424). Total length 8.8 mm. Carapace 3.5 mm long, 2.6 wide in thoracic region, 1.5 wide behind posterior lateral eyes. First femur 2.3 mm, patella and tibia 2.7, metatarsus 1.5, tarsus 0.7. Second patella and tibia 2.4 mm, third 1.5, fourth 2.4. Femora shorter than corresponding patellae and tibiae.

Diagnosis. This species differs from *C. nodosa* by the shape of the median plate of the epigynum (Figs. 421, 422).

Natural History. The web was vertical, 17.6 mm in diameter and 130 cm above the ground. It had 26 radii (G. Alayon, personal communication).

Distribution. Cuba (Map 6F); no other specimens were found.

Cyclosa nodosa (O. P.-Cambridge)
Figures 425–429; Map 6F

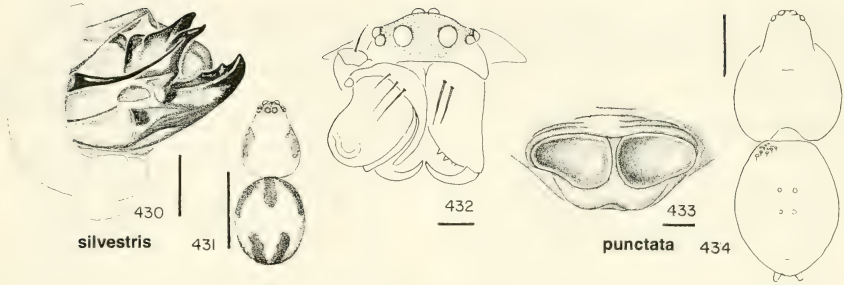
Turckheimia nodosa O. P.-Cambridge, 1889: 47, pl. 4, fig. 11, imm. Immature holotype from Chicoyoito, Guatemala, from citron tree, in BMNH, examined.

Cyclosa nodosa:—F. P.-Cambridge, 1904: 496, pl. 47, fig. 11, ♀, Roewer, 1942: 760. Bonnet, 1956: 1320.

Note. Although immature, *Turckheimia nodosa* was considered a separate species by F. P.-Cambridge because the abdomen is square; that of *C. diversa* longer than wide.

The name Chicoyoito is not in Selander and Vaurie (1962) but Chicoy is, located in the Alta Verapaz Province, Guatemala.

Description. Female from Costa Rica. Carapace dark brown with median light line on thorax (Fig. 427). Sternum dark brown with median white line. Abdomen white with dorsal, symmetrical, dark, lightly sclerotized patches (Fig. 427); venter black with indistinct, small transverse white marks in center (Fig. 428). Abdomen with a pair of spherical tubercles anterior and one posterior, the posterior median pointed, all hirsute (Figs. 427–429). Total length 9.5 mm. Carapace 3.7 mm long, 2.9 wide in thoracic region, 1.6 wide behind posterior lateral eyes. First femur 2.3 mm, patella and tibia 2.8, metatarsus 1.3, tarsus 0.4. Second patella and tibia 2.5 mm, third 1.7, fourth 2.7. All femora



Figures 430–432. *Metazygia silvestris* (Banks), male. 430, left palpus. 431, dorsal. 432, eye region, chelicerae and right palpus.
Figures 433, 434. *Cyclosa punctata* Keyserling, female. 433, epigynum. 434, dorsal.
Scale lines: dorsal 1.0 mm; Figures 430, 432, and 433 0.1 mm.

shorter than corresponding patellae and tibiae.

Variation. Total length of females 8.6 to 9.5 mm. One specimen had light bands around the dorsal sclerotized patches. The illustrations were made from specimens from Escazú, Costa Rica.

Diagnosis. This species is distinguished from *C. ojeda* and *C. tamanaco* by the oval to circular markings of the abdomen (Figs. 427–429). It differs from *C. alayoni* by having the median plate of the epigynum narrower (Figs. 425, 426).

Distribution. Guatemala to Costa Rica (Map 6F).

Specimens Examined. COSTA RICA *San José*: San Antonio de Escazú, 1,500 m, July 1987, 1♀ (W. Eberhard TL 2–3, MCZ). *Cartago*: Road to Conçepción de Tres Ríos, 1,300 m, Apr. 1979, 1♀ (W. Eberhard 1892, MCZ).

APPENDIX

Metazygia silvestris (Bryant) new combination
Figures 430–432

Larinia silvestris Bryant, 1942: 5, figs. 5, 7, 10, 11, ♂. Male holotype from Maricao Forest, Puerto Rico, 2,500 ft [830 m], in MCZ, examined. Brignoli, 1983: 272.

Description. Male holotype. Carapace yellow-white with black band on each side of thorax; black band truncate at both ends. Eye area black. Sternum with a yellow-black band around each side, fused posteriorly to form a black V. Legs yellow-white. Abdomen white with three anterior and posterior black bands (Fig. 431); venter yellowish white with a pair of indistinct black spots side by side. Posterior median eyes 0.8 diameter of anterior medians, laterals 0.7 diameter. Anterior median eyes 1 diameter apart, 0.5 diameter from laterals. Posterior median eyes 0.3 diameter apart, 1.1 diameters from laterals. Height of clypeus equals 0.6 diameter of anterior median eye. Abdomen oval (Fig. 431). Endite without tooth. Palpal patella with one macroseta. First coxa without hook. Total length 2.0 mm. Carapace 1.0 mm long, 0.8 wide in thoracic region, 0.5 wide behind posterior lateral eyes. First femur 1.1 mm, patella and tibia 1.5 (metatarsus and tarsus lost). Second patella and tibia 1.4 mm, third 0.8, fourth 0.9.

Diagnosis. The proximity of the posterior median eyes (Fig. 431), the oval abdomen (Fig. 431), and the single macroseta of the palpal patella (Fig. 432) places the species in *Metazygia*. The shape of the median apophysis, conducter and terminal apophysis (Fig. 430) separates this male from species of *Cyclosa* and other *Metazygia* species. There are macrosetae on the edge of the cymbium (Fig. 432) and a pair

of macrosetae on the anterior margin of each chelicera (Fig. 432). These macrosetae are not found in males of other *Metazygia* species.

Cyclosa punctata Keyserling
Figures 433, 434

Cyclosa punctata Keyserling, 1880: 312, pl. 2, fig. 14, ♀. Female holotype, from Neu Freiburg, Brazil [Nova Friburgo, Est. Rio de Janeiro], in BMNH, examined. Keyserling, 1893: 271, pl. 14, fig. 201, ♀. Roewer, 1942: 760. Bonnet, 1956: 1322.

Description. Female holotype. Carapace, legs golden yellow. Abdomen white with tiny setae, each with a sclerotized reddish base (Fig. 434); venter with black and white patches. Posterior median eyes same diameter as anterior medians; anterior laterals 0.7 diameter of anterior medians, posterior laterals 0.9 diameter. Anterior median eyes 0.8 diameter apart, 0.5 diameter from laterals. Posterior median eyes with narrow canoe-shaped tapetum. Posterior median eyes 0.7 diameter apart, 1 diameter from laterals. Lateral eyes touching each other. Ocular trapezoid almost square, longer than wide, slightly wider in front than behind. Height of clypeus equals 1 diameter of anterior median eye. Abdomen oval (Fig. 434). Total length 5.7 mm. Carapace 3.7 mm long, 2.9 wide in thoracic region, 1.2 wide behind posterior lateral eyes. First femur 3.0 mm, patella and tibia 3.4, metatarsus 2.5, tarsus 1.1. Second patella and tibia 3.5 mm, third 2.4, fourth 3.7.

Diagnosis. This species is distinguished by its narrow eye region (Fig. 434) and by the epigynum with two depressions, T-shaped septum and posterior border (Fig. 433). It resembles *Gea* species, but lacks the procurved posterior median eye row. Placement of this species is uncertain. It may not be an araneid or tetragnathid.

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The Dentition, Systematics, and Phylogeny of *Pseudoxyrhopus* and Related Genera from Madagascar (Serpentes: Colubridae), with Descriptions of a New Species and a New Genus

JOHN E. CADLE

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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THE DENTITION, SYSTEMATICS, AND PHYLOGENY OF *PSEUDOXYRHOPUS* AND RELATED GENERA FROM MADAGASCAR (SERPENTES: COLUBRIDAE), WITH DESCRIPTIONS OF A NEW SPECIES AND A NEW GENUS

JOHN E. CADLE[1]

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ABSTRACT. *Pseudoxyrhopus oblectator* new species is described from Ranomafana National Park in southeastern Madagascar. This new species is characterized by having 21 midbody scale rows, a pale nape collar, and a dark brown or blackish dorsum with a narrow pale lateral stripe. It is most similar to *P. ambreensis* and *P. sokosoko*, but it differs from *P. ambreensis* in having eight supralabials with labials 4+5 touching the eye (seven with labials 3+4 touching the eye in *P. ambreensis*) and in details of the disposition of the pale lateral stripe. *Pseudoxyrhopus oblectator* differs from *P. sokosoko* in having a pale nape collar (absent in *P. sokosoko*).

Hemipenial and dental characters of *Pseudoxyrhopus* are reviewed, and some previous observations are corrected. Based on the new observations, relationships and previously erected species groups within *Pseudoxyrhopus* are reassessed. Hemipenes of

[1] Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138.

Pseudoxyrhopus are bilobed and are entirely spinose, with centrolineal sulci spermatici. Contrary to previous reports of a single maxillary fang in three species, all species of *Pseudoxyrhopus* have a pair of enlarged posterior maxillary fangs and some species and individuals lack a maxillary diastema.

The dentitions of *Pararhadinaea melanogaster, P. albignaci,* and *Heteroliodon occipitalis* are redescribed. Based primarily on substantive dental differences from *P. melanogaster, Exallodontophis* new genus is created to accommodate *"Pararhadinaea" albignaci* Domergue. *Exallodontophis* is characterized by an unusual maxillary dentition consisting of a pair of considerably enlarged teeth in the middle of the maxilla, followed by an exceptionally broad diastema and a pair of fangs. This arrangement is unlike that of any other Malagasy snake. Some dental characters previously attributed to *Pararhadinaea* were based on *Exallodontophis.* Although the dentition of *Pararhadinaea melanogaster* Boettger (type species of *Pararhadinaea*) is unusual in some respects, its maxillary and dentary dentition are unlike those of *Exallodontophis.* Present evidence suggests that *Exallodontophis* is more closely related to *Pseudoxyrhopus* than to *Pararhadinaea melanogaster.*

Several characters of the dentition provide synapomorphies suggesting relationships among *Pseudoxyrhopus, Exallodontophis, Heteroliodon, Pararhadinaea,* and other Malagasy colubrids. Hinged teeth are reported for the first time in all four genera, and this derived character is shared with *Liophidium. Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon* share, in addition, enlarged median dentary teeth, and in the former two genera these enlarged teeth are followed by a diastema. The dentary dentition of *Pararhadinaea melanogaster* is unique in having five or six greatly enlarged and widely spaced posterior teeth. The teeth in *Heteroliodon* and *P. melanogaster* are unusual in having blunt, anteroposteriorly compressed tips similar to teeth in species of *Liophidium.* Several unusual features of the dentition of *Pseudoxyrhopus, Heteroliodon, Exallodontophis,* and *Pararhadinaea,* including hinged teeth, enlarged median dentary teeth and diastema, and enlarged median maxillary teeth and broad diastema, are probably related to diets rich in skinks and/or gerrhosaurids. Known diets of *Pseudoxyrhopus* species include skinks, skink eggs, and rodents.

Hinged teeth and a modified pattern of tooth replacement support the relationship of *Liophidium* to *Pseudoxyrhopus, Heteroliodon, Exallodontophis,* and *Pararhadinaea,* in contrast to a recent hypothesis that the last four genera had no close Malagasy relatives. Consequently, the *Pseudoxyrhopus* group comprises five genera: *Pseudoxyrhopus, Exallodontophis, Heteroliodon, Pararhadinaea,* and *Liophidium.* A phylogenetic analysis of the *Pseudoxyrhopus* group based on morphological characters resulted in three equally parsimonious trees that differed in their placement of *Pararhadinaea.* One of the most parsimonious trees (MPTs) and the strict consensus of the three trees had the same topology: (((*Pseudoxyrhopus, Exallodontophis*), *Heteroliodon*), *Pararhadinaea, Liophidium*). In the other MPTs *Pararhadinaea* was the sister group to either *Liophidium* or to *Pseudoxyrhopus–Exallodontophis–Heteroliodon.* Some characters of the dentition in the *Pseudoxyrhopus* group are shared with mainland African species of *Lycophidion, Chamaelycus, Mehelya,* and putatively related genera (Group II of Bogert). However, other substantive differences between the African and Malagasy groups in dentition and hemipenial morphology suggest that the shared similarities in dentition may be convergences related to diet. Moreover, differences in the morphology of the hemipenes and dentition among some of the Group II genera suggest that additional investigation of the monophyly of this group is warranted.

INTRODUCTION

The Malagasy colubrid genus *Pseudoxyrhopus* includes 10 species of apparently relatively secretive snakes (Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). Six of the 10 species were described in the last century, but the other four have been described since 1993. Most species are known from relatively few specimens. During a survey of the herpetofauna of Ranomafana National Park (see Cadle, 1995, 1996a,b) an apparently new species of *Pseudoxyrhopus* was obtained and is described herein. The new species conforms to diagnoses of the genus *Pseudoxyrhopus* (Boulenger, 1893; Raxworthy and Nussbaum, 1994) in having a median series of enlarged dentary teeth, and it is phenetically very similar to several other species in the genus. However, no diastema precedes the posterior maxillary fangs, in contrast to the condition previously reported for other species of *Pseudoxyrhopus.*

In describing the new *Pseudoxyrhopus* I discovered two previously unreported dental characters for the genus (hinged teeth, dentary diastema). Moreover, existing descriptions of dentition in *Pseudoxyrhopus* and its presumed close relatives, *Heteroliodon* and *Pararhadinaea,* were incomplete and inaccurate to varying degrees. Thus, I provide here an extended discussion of these characters and correct errors in previous literature. The revised

understanding of variation in the dentition of these snakes required the creation of a new genus to accommodate *"Pararhadinaea" albignaci* because it possesses novel characters not present in the type species of *Pararhadinaea.* Until the new genus is diagnosed I use quotation marks when *albignaci* is associated with *Pararhadinaea* to call attention to this erroneous association. The new characters also bear on hypotheses of the relationships of these snakes to other Malagasy colubrids, and these implications are discussed.

MATERIALS AND METHODS

Taxa in the Study Group and Specimens Examined

The new species of *Pseudoxyrhopus* is known from three specimens. I compared other species of *Pseudoxyrhopus* based on descriptions in the literature (Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998; and references therein) and personal observations (see Specimens Examined). Revised understanding of some dental characters in *Pseudoxyrhopus, Heteroliodon,* and *Pararhadinaea* is based on study of holotypes of the nominal taxa *Heteroliodon occipitalis* (Boulenger), *"Pararhadinaea" albignaci* Domergue, *Pararhadinaea melanogaster* Boettger, and *Pararhadinaea melanogaster marojejyensis* Domergue in addition to some other specimens of these taxa. Although I later transfer *"Pararhadinaea" albignaci* Domergue to a new genus, the justification first requires review of previous descriptions of dentition in these snakes. Explicit reference to *Pararhadinaea* herein includes only the type species, *P. melanogaster* Boettger.

Although I concur with the close relationship among *Pseudoxyrhopus, Heteroliodon,* and *Pararhadinaea* postulated by Raxworthy and Nussbaum (1994), I also include *Liophidium* and a new genus created for *"Pararhadinaea" albignaci* in this assemblage. I refer to this putative clade of five genera as the *Pseudoxyrhopus* group.

Standard Taxonomic Characters

Hemipenial terminology follows Myers (1973, 1974) and Myers and Campbell (1981). Methods for hemipenial examinations were detailed by Cadle (1996a), including modification of the technique of Pesantes (1994) for everting hemipenes with lobes only partially everted upon preservation. Geographic coordinates for two localities, Ambodiamontana and Talatakely, were determined using a Trimble Scout© portable Geographic Positioning System. Other coordinates were determined from maps published by the Foiben-Taosarintanin'i Madagasikara (FTM), Antananarivo. Colors in life were taken from field notes and from color transparencies. Measurements (in millimeters) of head scales and head dimensions were made with dial calipers to the nearest 0.1 mm. Body measurements were made with a plastic ruler or meter stick to the nearest millimeter. Drawings of dentition were made with the assistance of a camera lucida mounted in a dissecting microscope. Museum abbreviations used in the text are identified at the beginning of the list of specimens examined.

Dorsal scale formulae are given as the number of scales at the level of the 10th ventral, at midbody, and 10 ventrals anterior to the vent (e.g., 19-21-19). The point of posterior reduction in the dorsal scales is given with reference to the corresponding ventral scale, expressed as the number of dorsal row(s) lost (−) or fused (+) followed by (in parentheses) the ventral scale corresponding to the point of reduction. For example, the formula −5(93) indicates loss of dorsal row 5 at the level of ventral 93; 4+5(93) indicates fusion of rows 4 and 5 at the level of ventral 93. Distinguishing between loss and fusion of dorsal rows is sometimes ambiguous, although fusions are usually indicated by two adjacent scales united by a partial suture. Left and right sides may vary in the position and nature (loss or fusion) of the reduction, which is thus given for both sides.

Maxillary and Dentary Dentition Formulae

Most of the species under consideration herein have a series of subequal maxillary teeth followed by a distinctly enlarged pair of ungrooved fangs. The word *fang* is used here in the sense of Myers (1974: 29) to refer to a large piercing tooth. Fangs in the *Pseudoxyrhopus* group may or may not be preceded by a diastema. Maxillary tooth formulae are given as the number of subequal teeth plus two fangs (e.g., 15+2) whether or not a diastema is present. Several species have an unusual pattern in which the maxillary teeth gradually increase in size anterior to posterior, but two or more enlarged posterior teeth may be present. In such cases the number of fangs is subjective and is discussed as necessary. I use the descriptor *dentitional* to refer to the morphology or variation in entire tooth rows or series of teeth.

Most systematic treatments of colubrids report a gap or diastema separating the posterior (often enlarged) teeth of the maxilla from the anterior teeth as present or absent. But this dichotomy obscures much variation in the width of the diastema that may have functional and/or systematic significance. Because of variation in the width of a space preceding the fangs in these and other snakes I have tried to be more precise in expressing this character. Operationally I consider a diastema to be present when there is a space large enough to accommodate an additional tooth of equivalent size to adjacent teeth in the jaw (excluding enlarged teeth such as fangs).

Even when a distinct maxillary diastema is present under this criterion, its width varies greatly. It is very narrow in some colubrids (no more than the width of the teeth anterior to the fangs), as in some species of *Liopholidophis* (Cadle, 1996a). In other species the diastema is very broad (e.g., 2–3 times the width of the teeth preceding it in some species of *Geodipsas*; Cadle, 1996b). The number, position, and width of maxillary diastemata may vary among species within a genus (e.g., *Rhadinaea*; Myers, 1974). The functional significance of this variation (if any) is unknown. However, recording the width of the diastema relative to the most posterior maxillary teeth in front of the fangs provides a useful means of making comparisons among species and avoids the ambiguity inherent in simply recording a gap. Such ambiguity probably accounts for much of the confusing variation reported for the *Pseudoxyrhopus* group.

Pseudoxyrhopus and two other genera under consideration have two or more enlarged teeth in the middle of the dentary tooth row, which is sometimes followed by a diastema. To concisely express the pattern of this unusual dentary dentition I devised a dentary tooth formula with the form $a(b–c)De = f$, where a is the number of small teeth anterior to the median enlarged teeth; $(b–c)$ are the actual tooth numbers (range) of the median enlarged series; D indicates that a diastema follows the enlarged teeth (- in this position indicates no diastema); e is the number of teeth following the diastema (or enlarged series); and f is the total number of dentary teeth. In reality, the anterior dentary teeth of *Pseudoxyrhopus* gradually increase in size so that the range of the median enlarged series is somewhat arbitrary. Nonetheless, in most specimens examined three teeth seemed greatly enlarged over the others. In *P. tritaeniatus* the distinction is especially arbitrary (see Fig. 6), but teeth 6–8 are somewhat longer and more robust and have wider bases than the preceding teeth.

Phylogenetic Analyses

Phylogenetic trees were constructed using maximum parsimony implemented in PAUP 3.1 (Swofford, 1993). The branch-and-bound algorithm was used to insure that recovered trees were, indeed, maximally parsimonious. All characters were binary, unordered, and equally weighted. Terminal taxa were scored for each character as either of two states (0 or 1), poly-

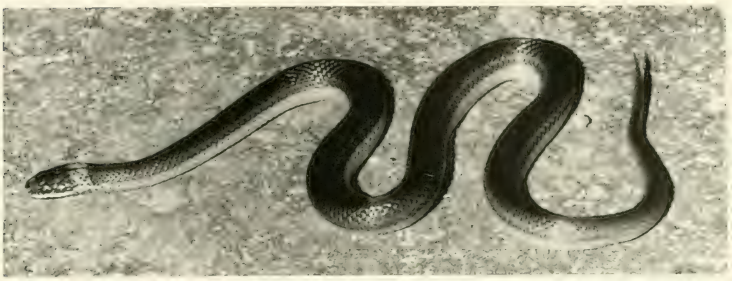

Figure 1. Holotype of *Pseudoxyrhopus oblectator* (MCZ 182292) new species, in life. Approximately ×0.7.

morphic (01), or uncertain (?). Both ACCTRAN and DELTRAN character optimizations (accelerated and delayed transformation, respectively) were employed. An explicit outgroup for rooting purposes was not available for the study group. Trees were rooted using an artifical ancestor whose states for some characters were inferred when the ancestral state for the ingroup (the *Pseudoxyrhopus* group) seemed clear based on consideration of likely outgroups. Other characters in the ancestor were coded as uncertain (?) when the ancestral state of the ingroup could not be reliably inferred. The argumentation for each character state in the hypothesized ancestor is provided in the character discussions; alternative codings for some terminal taxa were used for several characters. Alternative trees were evaluated in terms of overall length (total number of steps) and two measures of correspondence between data and the trees: the consistency index (CI), which was calculated after excluding uninformative characters, and the retention index (RI). Trees of minimal length (most parsimonious trees [MPTs]) were considered the best estimates of phylogenetic relationships. Explicit alternative phylogenetic hypotheses were tested by using a constraint tree that maintained the monophyly of a particular group of interest while allowing all other ingroup taxa to vary in position. The lengths of MPTs obtained with and without constraint were compared.

Figure 2. Head and anterior body of *Pseudoxyrhopus oblectator* (MCZ 182292; holotype) new species, in life. Approximately ×1.25.

DESCRIPTION OF A NEW SPECIES OF *PSEUDOXYRHOPUS*

Pseudoxyrhopus oblectator new species

Figures 1, 2, 4, 5, 17

Holotype (Figs. 1, 2, 17). MCZ 182292 (field number JEC 14923), an adult male collected 10 January 1998 from Mahajo Stream (a southern tributary of the Ranomena River), Ranomafana National Park (northern sector), Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar; 1,110 m elevation [approximately 21°13′S, 47°28′E]. John E. Cadle, Talata Pierre, and Rajeriariason Emile, collectors.

Paratype. MCZ 181287 (JEC 11467), a juvenile male collected 27 December 1991 by J. E. Cadle from a pitfall trapline at Talatakely, Ranomafana National Park, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar, 950 m elevation [21°15′50″S, 47°25′10″E].

Referred Specimen. MCZ 180299 (JEC 12722), an adult male collected 15 February 1993 by Dan Turk at Ambodiamontana (6 km W Ranomafana at entrance to Ranomafana National Park), Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar, 910 m elevation [21°15′20″S, 47°25′18″E]. MCZ 180299 is a badly damaged roadkill and is somewhat desiccated, but all scale counts were determinable. The damaged skull of this specimen was removed for osteological examination. No specimens are known aside from the types and referred specimen.

Distribution (Fig. 3). Known from 900–1,100 m elevation near the type locality. The three known localities are within 10 km (airline) of one another within the Ranomafana National Park.

Etymology. The specific epithet, *oblectator,* is a masculine Latin noun in apposition meaning charmer, delighter, or pleaser. Most species of *Pseudoxyrhopus* are infrequently encountered and the epithet refers to the delight these uncommon snakes bring when they are found.

Diagnosis. Pseudoxyrhopus oblectator is characterized by having a pale nape collar in juveniles and adults, 21 midbody scale rows, fewer than 160 ventrals (known range, 143–158), fewer than 50 subcaudals (known range, 44–48), all subcaudals paired, and eight supralabials (4+5 contacting the eye). Coloration is dark brownish black middorsally, a pale lateral stripe on scale rows 4+5 at midbody (involving other rows elsewhere), and pale coloration on the lower three dorsal scale rows. Because few specimens (and no females) are known, ventral and subcaudal counts may be expected to vary somewhat from these values.

No species of other genera in the *Pseudoxyrhopus* group have 21 scale rows. Five other species of *Pseudoxyrhopus* have 21 midbody scale rows: *P. ambreensis, P. analabe, P. heterurus, P. quinquelineatus,* and *P. sokosoko* (Nussbaum et al., 1998). *Pseudoxyrhopus analabe* differs from *P. oblectator* in having all subcaudal scales undivided (entire). In *P. heterurus* the anterior subcaudals are undivided and the posterior ones are divided. *Pseudoxyrhopus quinquelineatus* differs from *P. oblectator* in having a rather pointed snout and countersunk lower jaw (rounded snout and normal lower jaw in *P. oblectator*) and a pale brown or yellowish dorsum with five narrow dark lines (blackish brown without dark lines in *P. oblectator*). *Pseudoxyrhopus oblectator* is most similar to *P. ambreensis* and *P. sokosoko.* All three species have 19-21-19 dorsal rows and the posterior reduction occurs by loss of row 5.

Pseudoxyrhopus oblectator and *P. ambreensis* are similar in having a pale nape collar, similar scale counts, a light lateral line on a dark dorsum, and pale lower dorsal scales. The two most distinct differences between these species are the number of supralabial scales (eight with 4+5 touching the eye in *P. oblectator,* seven with 3+4 touching the eye in *P. ambreensis*) and the disposition of the pale lateral stripe. In both species the pale stripe is less distinct anteriorly than posteriorly (Raxworthy and Nussbaum [1994] stated that the stripe began at midbody in *P. ambreensis,* but the stripe was evident all the way to the neck in preserved specimens I examined under magnification). In *P. oblectator* the stripe occupies dorsal row 5 the length of the body. Anteriorly it is more or less restricted to row 5, broadening to include the upper half of row 4 at the point where the dorsal count increases to 21 and broadening again toward the posterior end of the body to include the lower half of row 6. In *P. ambreensis* the lateral stripe occupies row 5 anteriorly, row 6 at midbody, and row 5 posteriorly; except for irregular involvement of parts of rows 4 and 6 posteriorly, the stripe in *P. ambreensis* is usually less than one scale row wide (reduced to series of dashes anteriorly). Thus, the lateral stripe is broader in *P. oblectator* than in *P. ambreensis.* In *P. oblectator* the stripe continues onto the tail, where it broadens to occupy virtually the entire lateral surface (Fig. 1); in *P. am-*

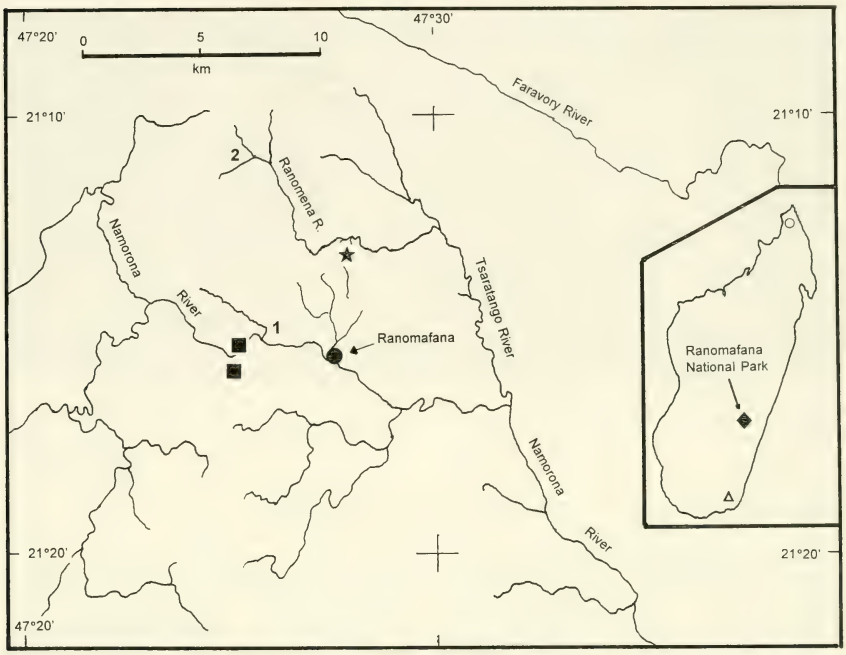

Figure 3. Distribution of *Pseudoxyrhopus oblectator*. Map detail is the central portion of Ranomafana National Park and vicinity. ★ = type locality of *P. oblectator*, ■ = other known localities for *P. oblectator*, ● = town of Ranomafana. Localities mentioned in the text: 1 = the village of Ambatolahy; and 2 = the approximate western edge of the Ranomena River swamps. *Inset:* Location of Ranomafana National Park and the distributions of *P. ambreensis* (○) and *P. sokosoko* (△); for these species symbols represent multiple contiguous localities (see Raxworthy and Nussbaum, 1994, for specific localties).

breensis the lateral stripe ends at the level of the vent (see Fig. 13; Raxworthy and Nussbaum, 1994; personal observations).

Several other more subtle features potentially distinguish *Pseudoxyrhopus oblectator* and *P. ambreensis*. The color of the nape collar is described as pale brown in life in *P. ambreensis* (Raxworthy and Nussbaum, 1994), whereas it was pale orange in the adult specimens of *P. oblectator*. However, too few specimens are accompanied by coloration data to be sure that this difference is consistent. *Pseudoxyrhopus oblectator* also has a slightly larger eye than *P. ambreensis* (0.30–0.34 times head depth versus 0.20–0.25 times head depth), but these measurements are rough guides only because head measurements lack precision. The difference is readily apparent by comparison of specimens side by side.

Pseudoxyrhopus sokosoko lacks a pale nuchal collar, whereas a collar is present in *P. oblectator*. *Pseudoxyrhopus oblectator* and *P. sokosoko* are very similar in scale counts and the position of the pale lateral stripe. In the type specimen of *P. sokosoko* (fide Raxworthy and Nussbaum, 1994) and in UMMZ 203660 the stripe is on scale rows 4+5 posteriorly but is not evident anteriorly. In two other specimens (UMMZ 203661, 209689) the stripe is evident under magnification from the neck to the tail

TABLE 1. SCALE COUNTS, MEASUREMENTS, AND OTHER DATA FOR THREE SPECIMENS OF *PSEUDOXYRHOPUS OBLECTATOR*. BILATERAL COUNTS (E.G., HEAD SCALES AND POSTERIOR SCALE REDUCTION) ARE GIVEN FIRST FOR THE LEFT SIDE, THEN FOR THE RIGHT.

	MCZ 182292 (holotype)	MCZ 180299	MCZ 181287
Sex	male	male	male
Total length (SVL[1]) (mm)	392 (325)	407 (329)	178 (143)
Tail length (mm)	67	78	35
Tail length/total length	0.17	0.19	0.20
Maxillary teeth	14+2	17+2 16+2	16+2
Dorsal scales	19-21-19	19-21-19	19-21-19
Ventral scales	158	146	143
Subcaudal scales	44	47	48
Posterior scale reduction	−5(93) −5(94)	−5(100) −5(100)	−5(73) −5(74)
Anal scale	divided	divided	divided
Preocular scales	1, 1	1, 1	1, 1
Postocular scales	2, 2	2, 2	2, 2
Temporal scales			
Anterior	1, 1	1, 1	1, 1
Posterior	2, 2	2, 2	2, 2
Supralabial scales (touching eye)	8, 8 (4+5)	8, 8 (4+5)	8, 8 (4+5)
Infralabial scales	9, 9	9, ?	9, 9

[1] SVL = snout–vent length.

and has a slightly different distribution from that of *P. oblectator*: anteriorly on scale row 5, rows 5 and 6 at midbody (rows 4 and 5 in *P. oblectator*), and posteriorly broadening to include row 5 and adjacent portions of rows 4 and 6 as in *P. oblectator*.

Data on the Holotype. The holotype is a well-preserved male with everted hemipenes (the left one removed for illustration) whose identifying characteristics are given in Table 1. The specimen is probably an adult, as indicated by somewhat convoluted vasa deferentia and mineralized hemipenial spines (for discussion, see Cadle, 1996b: 43–44).

Description. Meristic data and measurements for the three known specimens are reported in Table 1. The following description is based on all three specimens except that measurements of eye and head proportions for MCZ 180299 were not included (head damaged). Largest specimen MCZ 180299 (male, 329 mm snout–vent length [SVL]). No female available. Tail relatively short, 17–20% of total length. Dorsal scales smooth, lacking apical pits, and in 19-21-19 rows. Posterior reduction by loss of row 5. Ventrals 143–158, anal plate divided, subcaudals 44–48 and all paired.

Rostral scale slightly visible from above, 1.5–1.8 times wider than high. Paired internasals wider than long, each about half the size of a prefrontal. Paired prefrontals wider than long. Frontal roughly hexagonal in the adults (anterior angle very obtuse) but pentagonal in the juvenile. Frontal 1.2–1.6 times the length of the interparietal suture and 1.3–1.4 times longer than the distance from its anterior edge to the tip of the snout. Each parietal about 1.5 times longer than broad. Nasal divided posterior to nostril by a ventral suture and a shorter dorsal suture. Loreal small, squarish. One preocular, two postoculars; temporal series 1+2. Supralabials eight, with 4+5 touching the eye. Infralabials nine, the first pair in contact behind the mental; the first four infralabials broadly in contact with the anterior genials and the fifth infralabial contacting them narrowly or at a point. Anterior genials slightly long-

Figure 4. Maxillary dentition of *Pseudoxyrhopus oblectator* new species (MCZ 180299). Digital photograph of the posterior end of the right maxilla showing lack of a diastema in this species. Teeth are detached anterobasally, a manifestation of the fibrous hinge attaching the teeth on their posterior edges (see text). The posterior fang is missing from this specimen; its socket is in the lunate space posterodorsal to the anterior fang. Scale bar = 1 mm.

er than posterior genials; only the fifth infralabial contacts the posterior genials. No scale organs or pits visible on head scales.

Overall body form slender but robust. Head slightly wider than neck. Ventrolateral edge of body rounded. Pupil round. Eye small, about 0.3 times head depth at the middle of the orbit in adults, about 0.1 times head length (tip of snout to tip of retroarticular process), and about 0.85 times the distance from its anterior edge to the posterior edge of the nostril.

A pale nape collar in juveniles and adults (white in the juvenile, orange in the adults). Dorsum dark brown to black with a pale lateral stripe (on dorsal scale rows 4+5 at midbody) from the neck to the tip of the tail and pale lower dorsal rows. Venter light colored with fine dark stippling.

Dentition Fig. 4). Maxillary teeth 14-17+2, the rear fangs greatly enlarged and ungrooved; posterior fang slightly offset laterad. No diastema between the fangs and the more anterior teeth. Fangs strongly compressed (anterior edge broader than posterior) and with a knifelike posterior edge. Additional tooth counts from the prepared skull of MCZ 180299: palatine teeth 13-12; pterygoid teeth 21-21; dentary teeth 17 on the right (left dentary broken). Maxillary teeth except for the fangs and dentary teeth except for the enlarged median series are hinged in the sense of Savitzky (1981).

The first six dentary teeth of MCZ 180299 gradually increase in size; teeth 7–9 are noticeably enlarged, followed by an abrupt transition to smaller teeth 10–17. Dentary formula 6(7–9)-8 = 17. No diastema in the dentary tooth row of MCZ 180299, but a dentary diastema large enough to accommodate about a single tooth is present in the holotype. On the right side of the holotype five small dentary teeth are followed by three greatly enlarged teeth (posterior dentary teeth not investigated). Anterior and posterior dentary teeth subequal.

Hemipenis (Fully Everted Left Organ of Holotype; Fig. 5). Deeply bilobed, noncapitate, entirely spinose (acalyculate). Sulcus spermaticus bifurcating just below the lobes and with centrolineal branches. Total length of everted organ 9.5 mm, bilobed for the distal 5.5 mm (58%). In overall form the organ has a slightly bulbous midsection but tapers gradually proximally and distally from that point. No basal pockets

or lobes. Ornamentation of both the asulcate and sulcate surfaces is similar. Basal area below the lobes with minute spines. At the level of the sulcus division the spines abruptly change to moderate sized, curved, mineralized spines. These spines continue to the tips of the lobes, gradually decreasing in size (i.e., proximal spines in this battery are the largest). Crotch of the organ between the lobes is nude, but distally the inner surfaces of the lobes are spinose. The lobes gradually taper toward their tips, which are blunt, with a few scattered minute spines (nearly nude), and rugose. Sulcus spermaticus a very deep groove with somewhat thickened borders. Spines present up to the edges of the sulcus. The sulcus ends in a dimple on the tip of each lobe where the retractor muscle attaches on the inside of the everted organ.

Coloration in Life (Holotype). Top of head somewhat reddish brown flecked with dark brown. Iris reddish brown or dull orange. Upper labials white, bordered above and below by a wavy dark brown or blackish line (Fig. 17). Rostral white; white irregular line extends from the rostral patch dorsally and posteriorly over the lateral edges of the internasals. Ventral surface of head dusky, heavily flecked with dark gray especially concentrated along the lip border, the mental scale, and genials; an irregular elongate white patch is present on each side of the throat on infralabials 4 and 5. The dark color of the ventral side of the head dissipates posteriorly, becoming a fine peppering over the entire venter concentrated toward the anterior edge of each ventral scale and denser on the anterior part of the body than more posteriorly. General aspect of venter light, washed with rose or pink. Nape collar orange dorsally, grading to dirty white on the side of the head; about three scales wide and extending from the posterior edge of the parietals onto the neck. Collar divided middorsally by a thin brown line extending from the parietals to the dark dorsal coloration on the body. Lateral scales within the collar with dark brown spots occupying ⅓ to ½ of the area of each scale (Fig. 2); other collar scales more finely flecked with dark brown.

Middorsum dark brownish black, somewhat lighter laterally. Narrow reddish orange lateral stripe disposed as follows: anteriorly on row 5 followed by rows 5 and 6, then rows 4 and 5 (midbody), and rows 4, 5, and 6 (posteriorly); these changes generally correspond to the changes in dorsal row numbers. At the level of the vent the stripe continues uninterrupted onto the tail, broadening to occupy most of the lateral surface of the tail (although heavily suffused with dark brown) and continuing to its tip. The lateral pale stripe is bordered ventrally by a regular dark brown line 1–1.5 scales wide. The lower 2.5–3 dorsal rows are dirty white anteriorly but washed with reddish orange on the posterior ⅔ of the body; these rows are flecked and spotted with dark brown.

The other adult male (MCZ 180299) was similar in coloration to the holotype, but the ventral wash was orangish rather than rose. The juvenile (MCZ 181287) was similar in coloration to the adults, but the nape collar and venter were white rather than orange or rose colored. Thus, like most species of *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994), *Pseudoxyrhopus oblectator* does not appear to undergo a significant ontogenetic change in coloration.

Coloration in Preservative. In preserved specimens, all the orange and rose colors fade to dirty white or pale brown and colors in general are duller.

HABITATS AND NATURAL HISTORY OF *PSEUDOXYRHOPUS OBLECTATOR*

All three specimens of *Pseudoxyrhopus oblectator* were collected during the rainy season at Ranomafana (roughly December–April). The holotype was found by day under a large log in relatively undisturbed upland primary rainforest. The juvenile (MCZ 181287) came from a hillside in selectively logged upland primary rainforest.

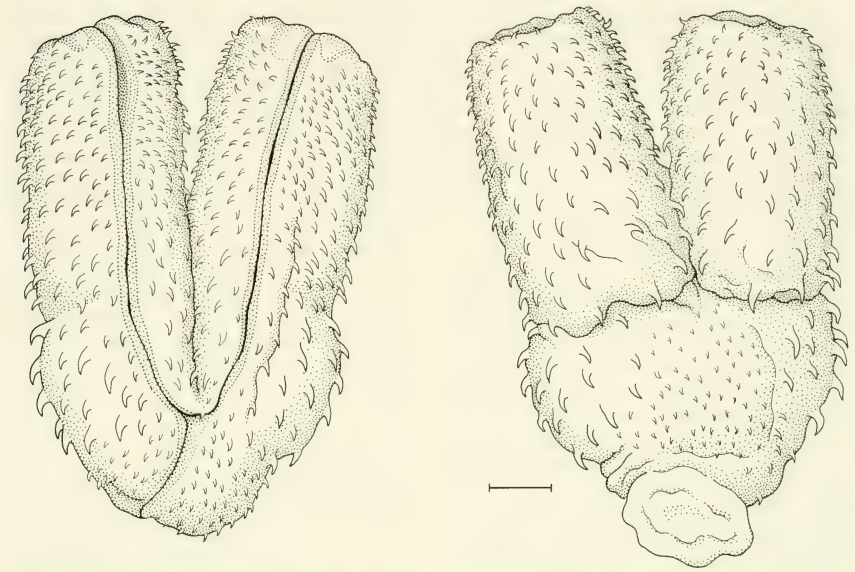

Figure 5. Hemipenis of *Pseudoxyrhopus oblectator* (holotype, MCZ 182292) in sulcate and asulcate views. Scale bar = 1 mm.

It was obtained from a drift fence and pitfall trapline set parallel to a trail in an area of broken canopy at the forest/trail ecotone. The snake was retrieved from the trap in the morning and had probably fallen in the previous night. MCZ 180299 was dead on Route National 25, a small road passing through habitats similar to those in which the other specimens were found. *Pseudoxyrhopus oblectator* is most likely nocturnal and/or secretive, as are all other species of *Pseudoxyrhopus* for which observations on activity exist (Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998).

Ranomafana National Park is divided by Route National 25 into a large northern sector and a smaller southern sector. The type locality of *Pseudoxyrhopus oblectator* is in the southeastern portion of the northern sector of the park, whereas the other two localities are in the southern sector in the vicinity of the Ranomafana Research Station at Talatakely (Fig. 3). The holotype was obtained during a backpacking exploration of the course of the Ranomena River and its western tributaries, beginning at the the village of Ambatolahy, traveling north to the western edge of the extensive riverine swamps along tributaries of the Ranomena River at approximately 21°12′36″S, 47°26′E (indicated on the 1:50,000 Ifanadiana topographic map produced by FTM), and thence south and east following the main course of the river (Fig. 3).

The Ranomena River is a west–east flowing river of moderate size that joins the Tsaratango River near the village of Bevohazo (the Ranomena River should not be confused with the Menarano River in the southern sector of Ranomafana National Park; both names mean "red water," referring to the dark rusty color of these blackwater streams). At approximately 21°13′07″S, 47°27′10″E, the Ranomena River passes over an escarpment with huge

boulders, cascading waterfalls, and an abrupt drop in elevation. The type locality of *Pseudoxyrhopus oblectator,* along a small tributary of the Ranomena River called *Mahajo* (pronounced Mah-hah'-zhū) by local informants, is a short distance east of this precipice and south of the main course of the Ranomena River. The Mahajo ascends rather steeply away from the Ranomena River in this hilly terrain.

At the type locality Mahajo Stream is very shallow, amounting to rivulets of less than 30 cm basal depth (when not swelled by rains) meandering among boulders. It is 2–4 m wide, with white water and a substrate of sand, gravel, and scattered boulders. Slopes away from the stream are steep, well drained, and covered with forest containing many tree ferns, few *Pandanus* (Pandanaceae), and many hardwoods, principally *Ocotea* (Lauraceae) and trees referred to by their Malagasy names *maka* (probably *Dombeya* sp. [Sterculiaceae]; Heckel, 1910) and *tsinkotroka* (Melastomataceae; probably *Dichaetanthera* sp.; Heckel, 1910). Very few polysandra (*Dahlbergia* sp.), a major commercial hardwood, were present, probably because of prior and continuing exploitation of this tree in the area. Habitats at the localities where the other two specimens were taken are similar to those at the type locality but slightly more disturbed by old (>50 years) selective logging. All three localities are characterized by steep, well-drained slopes and have whitewater streams in the uplands, although the two major rivers near the known localities (the Ranomena and the Namorona) are blackwater. None of the specimens of *Pseudoxyrhopus oblectator* was closely associated with streams.

One dietary record is available for *Pseudoxyrhopus oblectator.* The juvenile (MCZ 181287; SVL = 143 mm, head width = 5.1 mm) had eaten five eggs of *Amphiglossus melanopleura* (Squamata: Scincidae) containing full-term embryos. All embryos were within their shells (egg diameters 5.75–6.25 mm), fully developed (with complete pigmentation), and probably close to hatching; two embryos removed from their shells for identification still had hemipenes everted. This probably constitutes one entire clutch of eggs; two gravid females of *A. melanopleura* from the Ranomafana area contained four and five shelled eggs, respectively (personal observations; a large clutch size for such small lizards!).

Neither of the two specimens of *Pseudoxyrhopus oblectator* collected alive showed any attempt to bite or struggle significantly. This behavior is similar to that of all specimens of *P. tritaeniatus* that I have observed alive—they are docile, inoffensive snakes and often slow moving even when handled.

HEMIPENIAL MORPHOLOGY OF *PSEUDOXYRHOPUS*

No hemipenes of *Pseudoxyrhopus* have been described previously. In addition to *Pseudoxyrhopus oblectator,* I examined hemipenes of three other species in detail: *P. ambreensis* (UMMZ 200061; everted), *P. sokosoko* (UMMZ 209689; in situ, retracted), and *P. tritaeniatus* (MCZ 182468; everted). A hemipenis of *P. kely* (UMMZ 192022; in situ, retracted) was examined externally for proportions only. This specimen, a paratype of *P. kely,* was reported as a female by Raxworthy and Nussbaum (1994), but its hemipenes are evident through a previous slit in the tail and small, immature testes are visible through a previous slit in the body. The specimens of *P. sokosoko* and *P. kely* are juveniles; the others are adults.

Hemipenes of all species are very similar in overall morphology, ornamentation, and sulcus position. The description given for the hemipenis of *P. oblectator* (Fig. 5) could suffice as a general description for any of the other species examined in detail except for slight proportional differences. In fact, the detailed similarity among the species is quite remarkable. The tips of the sulcus spermaticus appear to end in a dim-

ple in three species (*P. oblectator, P. tritaeniatus,* and *P. ambreensis*; configuration unclear in the retracted juvenile organ of *P. sokosoko*). This somewhat unusual feature may be characteristic of the genus; it does not appear to be an artifact of incomplete eversion.

The hemipenis of *Pseudoxyrhopus ambreensis* is 10.5 mm total length and bilobed for the distal 4.5 mm (43% bilobed). The hemipenis of *P. tritaeniatus* is 17 mm total length and bilobed for the distal 5 mm (29% bilobed). Of the species examined, the hemipenis of *P. tritaeniatus* has a more bulbous midsection and the shortest lobes. The retracted hemipenis of *P. sokosoko* extends to the level of the suture between subcaudals 4 and 5, dividing about the middle of subcaudal 2 (total length 4.6 mm, bilobed for the distal 3 mm [65%]). The spine ornamentation in *P. sokosoko* appears similar to that in the other species, although because the specimen is a juvenile the spines are nonmineralized and the specific pattern is difficult to discern. The retracted left hemipenis of *P. kely* extends to the level of the suture between subcaudals 5 and 6, dividing at the level of the suture between subcaudals 2 and 3 (total length 3.4 mm, bilobed for the distal 1.8 mm [53%]).

Although it is difficult to compare proportions of everted and retracted hemipenes, *Pseudoxyrhopus oblectator, P. kely,* and *P. sokosoko* have more deeply bilobed hemipenes (53–65%) than do the other two species (29–43%).

MAXILLARY TOOTH FORMULAE IN *PSEUDOXYRHOPUS*

Raxworthy and Nussbaum (1994) recognized four species groups of *Pseudoxyrhopus* (A–D) based on characters of the maxillary and dentary dentition and later included body size and the number of dorsal, ventral, and subcaudal scales in group definitions (Nussbaum et al., 1998). Although these groups were stated to be explicitly phenetic, Raxworthy and Nussbaum (1994) and Nussbaum et al. (1998) used the group characters to infer relationships among the species of *Pseudoxyrhopus.* My study revealed several characters recorded erroneously by previous authors. In this and the next sections I correct these observations, reinterpret several characters, and point out additional characters that may bear on relationships within *Pseudoxyrhopus.* I revisit relationships hypothesized by Raxworthy and Nussbaum (1994) and Nussbaum et al. (1998) in the context of evaluating the relationships of *Pseudoxyrhopus oblectator.*

A character used by Raxworthy and Nussbaum (1994) to distinguish species in Group A from the others was the presence of only a single enlarged posterior maxillary fang rather than two. I am aware of no other rear-fanged colubrids reported to have a single rear fang (or socket), although three fangs are present in some species (e.g., *Boiga* species; see, Bogert, 1940) and multiple enlarged rear teeth are present in some species of *Liophidium.* Because *Pseudoxyrhopus oblectator* has two enlarged posterior maxillary teeth but is otherwise very similar to *P. ambreensis* (Group A), I reevaluated the dentitional characters of the species readily available (Table 2). My reevaluation suggests that interpretations of a single posterior maxillary fang in two species of Group A (*P. ambreensis, P. kely*) are erroneous. The same is probably true of the other species of Group A (*P. analabe*), but the only known specimen has not been reexamined.

Based on UMMZ 200061, Raxworthy and Nussbaum (1994: 4) reported the maxillary dentition of *Pseudoxyrhopus ambreensis* as "12+1 maxillary teeth, the posteriormost tooth considerably enlarged and separated by a gap from the anterior 11 teeth." They indicated that *P. ambreensis* was "unusual compared to most other *Pseudoxyrhopus* species in that there is just a single enlarged posterior maxillary tooth rather than two." This was the con-

TABLE 2. DENTITIONAL VARIATION AMONG SPECIES OF *PSEUDOXYRHOPUS*. FEWER DENTARIES WERE EXAMINED THAN MAXILLAE.

Species	Maxillary teeth		Dentary teeth		Maxillary diastema	
	Formula[1]	*n*[2]	Formula[1]	*n*	Size[1]	*n*
P. ambreensis	15+2	2	5 (6–8) D10 = 18	1	absent	1
	14+2	1			=1 tooth	1
	13+2	1			≤1 tooth	1
P. imerinae	13+2	1	5 (6–8) D10 = 18	1	absent	1
P. kely	12+2	1	4 (5–7) D8 = 15	1	absent	1
P. microps	17+2	1	5 (6–8) D12 = 20	1	absent	1
P. oblectator	17+2	1	6 (7–9)-8 = 17[3]	1	absent	1
	16+2	2				
	14+2	1				
P. quinquelineatus	14+2	2	5 (6–8) D7 = 15	2	absent	2
	13+2	4	5 (6–8) D8 = 16	1	=1 tooth	1
			5 (6–7) D8 = 15	1	>1 tooth	2
			4 (5–7) D8 = 15	1		
P. sokosoko	12+2	1	5 (6–8) D10 = 18	1	=1 tooth	1
	15+2	1			≤1 tooth	1
P. tritaeniatus	15+2	2	5 (6–8) D13 = 21	3	absent	1
	16+2	3	5 (6–8) D12 = 20	1	≤1 tooth	2
					<1 tooth	1

[1]See Materials and Methods for explanation of scores.

[2]Number of specimens having a particular formula or diastema condition; these include observations made bilaterally on the same specimen (e.g., for skulls).

[3]Diastema variable.

dition later reported for *P. kely* and *P. analabe* (Raxworthy and Nussbaum, 1994: 14; Nussbaum et al., 1998: 130). These observations for *P. ambreensis* and *P. kely* are inaccurate. On the left side of UMMZ 200061 both fangs are still in place, although the posterior one is loose; on the right side, the anterior fang is missing and its empty socket is presumably the "gap" reported by Raxworthy and Nussbaum (1994); no diastema is present. Anterior to the pair of rear fangs in each maxilla of UMMZ 200061 are 15 teeth. The difference between my counts and those previously reported for this specimen (Raxworthy and Nussbaum, 1994) is probably due to failure to count empty tooth sockets or the small teeth at the anterior ends of the maxillae, which are easy to miss in small snakes. In general, my tooth counts are somewhat greater than those given by Raxworthy and Nussbaum (1994) when we have examined the same specimens. Thus, the correct maxillary tooth formula for UMMZ 200061 is 15+2 on each side.

At my request the maxillary fangs of the holotype of *Pseudoxyrhopus kely* (UMMZ 192021) were rechecked and Greg Schneider (in litt.) reported that the left side has two enlarged rear fangs, whereas the right side has one fang plus an empty socket. The paratype of *P. kely* (UMMZ 192022), which I examined, has a posterior fang in place on each maxilla and an empty socket for the other fang. Thus, I conclude that all species of *Pseudoxyrhopus* of Group A have the usual condition of two posterior fangs, in contrast to the claim that the group is characterized by a single fang.

Nonetheless, Group A of *Pseudoxyrhopus* is still characterized by the combination of relatively small size, low numbers of ventral and dorsal scales, fewer than 12 posterior dentary teeth, and a pale nuchal band (Nussbaum et al., 1998). However, none of these characters individually is unique to Group A and only the pale nuchal band distinguishes it from Group B. By these criteria *P. oblectator* belongs to phenetic Group A.

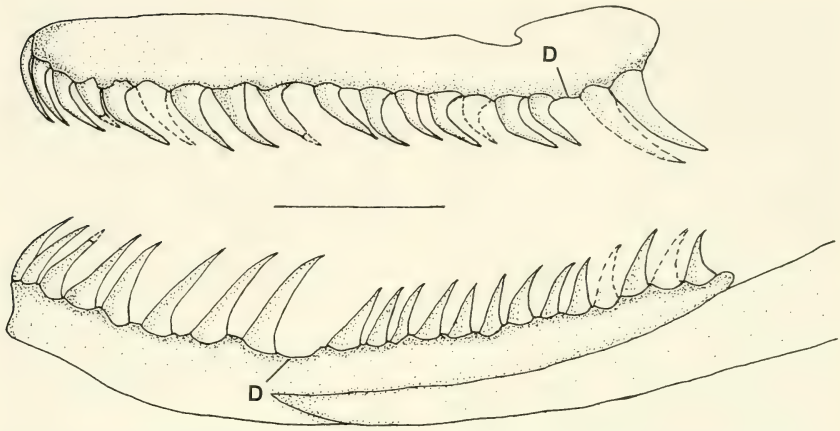

Figure 6. Left maxilla and right dentary (reversed) of *Pseudoxyrhopus tritaeniatus* (MCZ 182468). *D* = the diastemata in each tooth row. Teeth drawn with dotted lines are missing. Scale bar = 3 mm.

MAXILLARY AND DENTARY DIASTEMATA IN THE *PSEUDOXYRHOPUS* GROUP

In *Pseudoxyrhopus oblectator* the gap separating the anterior rear fang from the last small maxillary tooth is less than half the width of the tooth and approximately equivalent to the space between adjacent teeth in the rest of the maxilla (Fig. 4). Based on the criterion outlined *P. oblectator* lacks a diastema, a condition different from that reported for all other species of *Pseudoxyrhopus* (e.g., see Boulenger, 1890, 1893; Mocquard, 1909; Guibé, 1958; Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). Presence of a diastema is usually stated as a generic character for *Pseudoxyrhopus* (Boulenger, 1893; Raxworthy and Nussbaum, 1994). Thus, I reexamined the diastema in other readily available species of *Pseudoxyrhopus*.

In seven species of *Pseudoxyrhopus* studied, a maxillary diastema is either absent (some *P. ambreensis, P. kely, P. microps, P. oblectator*; some *P. quinquelineatus*) or very narrow (approximately equal to the width of a single tooth or less; some *P. ambreensis*, some *P. quinquelineatus, P. sokosoko, P. tritaeniatus*; Fig. 6). The broadest diastemata observed, 1–1.5 times the width of a tooth, were in two specimens of *P. quinquelineatus*.[2] Boulenger (1890), using crude diagrams, illustrated a maxillary diastema approximately the width of two teeth for *P. imerinae, P. microps*, and *P. quinquelineatus*. However, I examined maxillary dentition of all three species (Table 2) and each differs from Boulenger's illustrations. Both *P. microps* and *P. imerinae* lack a diastema, the space in front of the anterior fang being less than

[2] Charles W. Myers (in litt.) pointed out to me that some of the variation in diastema width could reflect differences in the number of prediastemal teeth—the more teeth the shorter the diastema within a species. My samples for species of *Pseudoxyrhopus* are too small to evaluate this hypothesis, but it does not seem to hold in *P. quinquelineatus*, for which six maxillary tooth counts varied only from 13 to 14 + 2. The broadest diastema (1.25–1.5 times tooth width) was in one specimen with 13 prediastemal teeth, whereas three other specimens with 13 teeth had no diastema. Nevertheless, the relationship between tooth numbers and diastema width bears additional (and more quantitative) study.

the width of a tooth. Variation in the width of the diastema is greatest among specimens of *P. quinquelineatus*. In this species the width of the diastema varies from less than one tooth to approximately 1.5 teeth. Of course, differences between Boulenger's observations and mine could represent intraspecific variation (or simply the crudeness of Boulenger's diagrams). However, given that the width of the diastema varies intraspecifically in *P. ambreensis* and *P. quinquelineatus* (Table 2), other species may vary as well (aside from *P. quinquelineatus* no species is represented by more than three observations). In all species of *Pseudoxyrhopus* the impression of a diastema is created by the posterior projection of the fangs adjacent to the vertically projecting teeth anterior to them (Figs. 4, 6). Detailed examination of the tooth bases is necessary for proper interpretation of the diastema. This morphology and the mistaking of empty sockets for a diastema probably account for previous recordings of a diastema in all species of *Pseudoxyrhopus* (e.g., Raxworthy and Nussbaum, 1994).

All species of *Pseudoxyrhopus* for which the dentary teeth were examined (*P. ambreensis, P. imerinae, P. kely, P. microps, P. oblectator, P. quinquelineatus, P. sokosoko, P. tritaeniatus*; Table 2) and *"Pararhadinaea" albignaci* have a previously unreported short diastema in the dentary tooth row separating the last of the median enlarged teeth from the following series of small dentary teeth (Fig. 6). Such a diastema was not present in *Heteroliodon occipitalis*. In *Pararhadinaea melanogaster*, the posterior four or five dentary teeth are separated by broad spaces, although none is discrete enough to be called a diastema.

The dentary diastema in *Pseudoxyrhopus* ranges from slightly smaller to slightly greater than the width of the large tooth preceding it but is always clearly larger than the spaces between the other dentary teeth. The diastema was narrowest in *P. oblectator*, in which a narrow dentary diastema was present in the holotype but not in the prepared skull of MCZ 180299. Thus, this character may vary intraspecifically (in general, I had only a single observation per species), although each of six dentaries (four specimens) of *P. quinquelineatus* had a distinct dentary diastema. Diastemata are not common in colubrid dentary tooth rows, although very broad ones are found in some, such as *Lycophidion* (Parker, 1933; Savitzky, 1981) and *Lycodon* (Smith, 1943).

Some variation in tooth form and proportions exists among species of *Pseudoxyrhopus*. For example, in the large species, *P. tritaeniatus* and *P. microps*, the teeth are relatively longer, more strongly curved, and more sharply pointed than in the smaller species (cf. Figs. 4, 6). In *P. tritaeniatus* the anterior maxillary teeth are slightly longer than the posterior ones (excluding fangs) (Fig. 6), whereas the opposite trend occurs in other species (e.g., *P. quinquelineatus*), and maxillary teeth are more or less subequal in still others. The fangs of all species of *Pseudoxyrhopus* are compressed to a greater or lesser extent, with a rounded anterior edge tapering to a narrow posterior edge. In some species the posterior edges of the fangs bears a slightly raised keel (e.g., *P. tritaeniatus*), whereas in others a broad knifelike ridge occurs posteriorly (e.g., *P. oblectator, P. ambreensis*).

All species of *Pseudoxyrhopus* examined have three distinctly enlarged median dentary teeth (Table 2), a character used in part to diagnose *Pseudoxyrhopus* (Boulenger, 1893; Raxworthy and Nussbaum, 1994). In most species these teeth are distinctly larger than the teeth anterior and posterior to them. However, in *P. tritaeniatus* the enlarged dentary teeth are not so distinguished in size from the anterior teeth (Fig. 6) (in the *P. microps* examined the anterior dentary teeth were missing). This size similarity results from the fact that the anterior dentary teeth are already large and the transition to enlarged teeth occurs in the first two or three teeth in the series. Thus, in *P. tritaeniatus* the distinc-

tion between the enlarged dentary series and the more anterior teeth is arbitrary. The same pattern of relative tooth size especially enhances the size distinction between the anterior (large) and posterior (small) dentary teeth in *P. tritaeniatus* (Fig. 6). Although the size difference between the anterior and posterior dentary teeth is sometimes stated as a "generic character" in *Pseudoxyrhopus* (e.g., Raxworthy and Nussbaum, 1994), it is most apparent in the large species and may not be evident at all in the small ones.

RELATIONSHIPS OF *PSEUDOXYRHOPUS OBLECTATOR* AND A RECONSIDERATION OF SPECIES GROUPS WITHIN *PSEUDOXYRHOPUS*

Nussbaum et al. (1998) characterized *Pseudoxyrhopus* species Group A (including *P. ambreensis, P. kely,* and *P. analabe*) as follows:

> small size (<238 mm SVL), low numbers of scale rows (19 or 21), low numbers of ventral (<154) and subcaudal (<54) scales, fewer than 12 dentary teeth posterior to the largest dentary tooth, a single enlarged posterior maxillary tooth, and a pale nuchal band.

The size range is an error because according to their own data (Nussbaum et al., 1998, table 1) *P. ambreensis* reaches 333 mm SVL. When corrected to reflect the presence of two rather than one fang, *Pseudoxyrhopus oblectator* conforms to this definition except for a slight difference in ventral count. The other species groups differ by lacking a nuchal collar (Group B), having more than 12 posterior dentary teeth, more dorsal scale rows, larger size, and more ventrals and subcaudals (Group C), or having a pointed snout and strongly overhanging rostrum (Group D).[3] However, there is no reason to expect that all these groups actually reflect nearest relationships. Groups A and B, for example, are distinguished only by the presence (A) or absence (B) of a pale nuchal collar.

As pointed out in the diagnosis, *Pseudoxyrhopus oblectator* is most similar to *P. ambreensis* (Group A) and *P. sokosoko* (Group B). *Pseudoxyrhopus ambreensis,* known only from extreme northern Madagascar (Fig. 3), is geographically remote from *P. oblectator* and *P. sokosoko* and differs from them in the disposition of the pale lateral stripe and in having a less divided hemipenis. However, the close similarity of *P. oblectator* and *P. sokosoko* (Group B) raises the possibility that these two are sister species, although any such suggestion is based on shared characters of uncertain polarity. The only substantive difference between *P. oblectator* and *P. sokosoko* is the presence (*P. oblectator*) or absence (*P. sokosoko*) of a nuchal collar. The two species are virtually identical in

[3] Group D includes *Pseudoxyrhopus imerinae* and *P. quinquelineatus.* Based on Boulenger's (1890) illustrations of dentition in these species, Raxworthy and Nussbaum (1994) and Nussbaum et al. (1998) included the presence of 12 or more posterior dentary teeth in the definition of Group D (Boulenger showed 12 posterior dentary teeth [18 total] for each species). My observations for these species differ. Four specimens of *P. quinquelineatus* (six dentaries, including two prepared skulls) have either seven or eight posterior dentary teeth, and one specimen of *P. imerinae* had 10 posterior dentary teeth (Table 2). Boulenger's (1890) primary concern was calling attention to the anterior enlarged dentary teeth in *Pseudoxyrhopus.* As suggested elsewhere with respect to the maxillary diastema, his figures are highly diagrammatic and may not be accurate with respect to tooth number and placement, as suggested, for example, by the wide spacing among the anterior dentary teeth in Boulenger's diagrams and his failure to indicate the dentary diastema that is present in each of these species. Given the highly schematic nature of these figures, Boulenger may have intended to show the general pattern and not the precise count of the posterior dentary teeth. In any case, whether the variation were 7–12 posterior dentary teeth, or some smaller variance around 7, this character does not apply to define Group D as used by Raxworthy and Nussbaum (1994) and Nussbaum et al. (1998). Although the number of dentary teeth is expected to vary just as maxillary tooth number, an intraspecific range of 7–12 posterior teeth seems large. However, *P. imerinae* and *P. quinquelineatus* have a pointed overhanging snout and unusual color pattern relative to other species of *Pseudoxyrhopus,* which suggests that they are sister species.

the disposition of the pale lateral stripe, they have the most deeply bilobed hemipenes of the species examined (58% and 65%, respectively), and they are similar in size, scale counts, and color pattern (except for the collar). *Pseudoxyrhopus sokosoko* is known from extreme southeastern Madagascar (Fig. 3) from lower elevations (≤800 m) than is *P. oblectator* (>900 m).

Pale nuchal collars are probably plesiomorphic within *Pseudoxyrhopus* inasmuch as collars are present in the presumed close relatives, *Heteroliodon*, "*Pararhadinaea*" *albignaci*, and *Pararhadinaea melanogaster*, and in 7 of the 11 species of *Pseudoxyrhopus* (in *P. microps* collars are present only in juveniles, and in *P. tritaeniatus* collars are variably present). Thus, the sharing of a collar by species of Group A provides no clear evidence of relationship. Because this character is the only one distinguishing Groups A and B, evidence for the interrelationships of these species must be sought in other characters. If *P. sokosoko* and *P. oblectator* are sister species and the interpretation of collars as plesiomorphic within *Pseudoxyrhopus* is correct, then collars have been lost independently in *P. sokosoko* and the other species of *Pseudoxyrhopus* that lack collars.

In contrast, Raxworthy and Nussbaum (1994) proposed that *Pseudoxyrhopus sokosoko* and *P. heterurus*, a widespread species of the eastern rainforests, are sister species comprising Group B. These species lack nuchal collars and have 21 scale rows, fewer than 12 posterior dentary teeth, and two enlarged maxillary teeth. Twelve or fewer posterior dentary teeth is a character also shared by the four species of Group A and other species, including at least *P. imerinae* and *P. quinquelineatus* (see footnote 3, Table 2). The other characters are widespread or universal within the genus. *Pseudoxyrhopus heterurus* differs from *P. sokosoko* in lacking a lateral stripe and having undivided anterior subcaudal scales and a larger body size. However, in *Pseudoxyrhopus heterurus* and *P. analabe* (Group A; Nussbaum et al., 1998) the subcaudals are wholly or partially undivided, an unusual (for colubrids) and ostensibly derived character that might indicate close relationship. This character argues more strongly for a *P. heterurus–P. analabe* relationship than do the characters linking *P. heterurus* and *P. sokosoko*.

Data presented herein challenge the maxillary and dentary tooth formulae originally used to characterize the species groups of *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). I suggest that some other characters (presence of a collar) are plesiomorphic and thus provide no evidence of relationship and that some other characters (entire subcaudals) bear further scrutiny for elucidating relationships within *Pseudoxyrhopus*. Any hypothesis of relationships within *Pseudoxyrhopus* currently depends on the relative significance attributed to characters such as the nuchal collar, lateral stripes, and scutellation differences. Certainly, with the revised definition of Group A proposed herein, the distinction between Groups A and B seems arbitary. However, the case for considering *P. imerinae* and *P. quinquelineatus* sister taxa seems secure because they share an unusual snout form and color pattern within *Pseudoxyrhopus*. Likewise, several characters shared by *P. tritaeniatus, P. ankafinaensis*, and *P. microps* seem to be apomorphic, thus supporting recognition of this group (Group C of Nussbaum et al., 1998) as a clade. However, the apomorphic nature of these shared characters is apparent only after proper interpretation of other dental characters of *Pseudoxyrhopus* and its relatives, which is the focus of the remainder of this report.

HINGED TEETH AND OTHER DIETARY SPECIALIZATIONS IN THE *PSEUDOXYRHOPUS* GROUP

Hinged Teeth

Among snakes hinged teeth have been previously reported in *Xenopeltis* (Xeno-

peltidae) and a small number of colubrid genera in the Neotropics, Africa, Madagascar, and southeast Asia (*Scaphiodontophis, Mehelya, Liophidium, Lycophidion, Sibynophis, Iguanognathus*) (Savitzky, 1981; Jackson et al., 1999).[4] In such teeth a fibrous connection between the base of each tooth and the jaw bone allows the teeth to be folded down. Their occurrence is correlated with a diet of hard-bodied lizard prey, such as skinks and gerrhosaurids (Savitzky, 1981, 1983). Among Malagasy snakes hinged teeth have previously been reported in several species of *Liophidium* (Savitzky, 1981). I here report their presence in *Pseudoxyrhopus, Pararhadinaea melanogaster, "Pararhadinaea" albignaci,* and *Heteroliodon occipitalis.* Detailed discussion of dentition in the last three is deferred to subsequent sections. In *Pseudoxyrhopus* hinged teeth are present in all species examined, but in *P. tritaeniatus* hinged teeth seem to be present in juveniles but not in the adults examined.[5]

These observations were prompted by examination of the maxillary dentition of the holotype of *Pseudoxyrhopus oblectator,* in which the teeth anterior to the fangs fold backward when pressed from the lateral or anterior surface with a needle. The dry skull of *P. oblectator* (MCZ 180299) is missing many of its teeth, but those that remain are detached on the anterobasal edge and deflected posteriorly; they appear to be attached basally on their posterior edges (Fig. 4). This configuration is very similar to that depicted for *Xenopeltis unicolor* and *Scaphiodontophis annulatus* (Savitzky, 1981, figs. 1C,G). The missing teeth of MCZ 180299 were probably lost because of their loose attachment at the jaw line and perhaps some deterioration prior to preservation (this snake was a roadkill). Using a fine needle as a probe, similarly mobile teeth were also found in *P. ambreensis, P. imerinae, P. kely, P. quinquelineatus,* and *P. sokosoko.* The specimen of *P. microps* examined was poorly preserved and had many teeth missing, but the anterior teeth in both the maxilla and dentary appeared to be somewhat kinetic, whereas posterior teeth were less so or even akinetic. Adults of *Pseudoxyrhopus tritaeniatus* appear not to have dental kinesis at all. In adult fluid-preserved specimens and dry skulls of this species the teeth are firmly ankylosed to the bones. However, dental kinesis was evident in a small juvenile of *P. tritaeniatus* (AMNH 60712; SVL 270 mm). To convince myself that the kinesis I observed in *Pseudoxyrhopus* was not some peculiar artifact of preservation I manipulated the dentition of many specimens of species in other

[4] Hinged teeth may be more widespread than realized among colubrids. Inspired by Parker's (1933) discussion of *Lycophidion* and *Chamaelycus* (=*Oophilositum* Parker), I inspected teeth in specimens of *Chamaelycus* and its presumed close relatives, *Hormonotus* and *Gonionotophis,* in addition to *Lycophidion* and *Mehelya* (see Savitzky, 1981). These genera comprise Group II of Bogert (1940). *Chamaelycus fasciatus* (MCZ 11165, 49605, 53461) and *C. parkeri* (MCZ 42687) also appear to have hinged teeth, whereas *Hormonotus modestus* (MCZ 5649, 22510) and *Gonionotophis granti* (MCZ 51813, 55358; MVZ 176439) do not. Parker (1933) reported two unidentified lizard eggs and Ineich (1998) reported a *Gerrhosaurus nigrolineatus* in stomachs of *Chamaelycus fasciatus.*

Edmond V. Malnate (in litt.) informed me that the Asian natricines *Amphiesma celebica* and *Tropidonophis truncatus* were skink feeders, and at his suggestion I examined the teeth of these species (MCZ 25267–69 and MCZ 33508, respectively). The teeth in both species are slightly blunt, which Malnate and Underwood (1988) suggested might be related to a diet of lizards with heavy osteoderms. In *A. celebica* a few teeth in the middle of the maxilla seemed to be hinged, but the three specimens examined had many missing teeth. However, in *T. truncatus* the teeth on approximately the anterior two-thirds of the maxilla are hinged. Thus, hinged teeth and other dental characters discussed herein are geographically widespread characters of colubrids feeding on lizards with dense osteoderms and have clearly evolved multiple times in the context of similar dietary regimes.

[5] Determination of dental kinesis must be done with fluid-preserved specimens. In dry skulls kinesis may be indicated by peculiar deflection of some teeth (e.g., Fig. 4) or by the appearance of an abscission line at the base of the teeth, but both of these features vary among preparations.

Malagasy colubrid genera collected on the same and different field trips as the *Pseudoxyrhopus*. In no case did I observe dental kinesis nor a modified tooth replacement (except in *Liophidium*), as observed in *Pseudoxyrhopus*.

The similarity of kinetic teeth (in fluid-preserved specimens) or anterobasally detached teeth (in dry skulls) in *Pseudoxyrhopus* and other hinge-toothed snakes (Savitzky, 1981) strongly suggests that the teeth of these species of *Pseudoxyrhopus* have a similar hinge mechanism (the connective tissue hinge is visible in histological and electron microscopic preparations). With few exceptions, the hinged condition in *Pseudoxyrhopus* appears to apply to all maxillary teeth except the fangs and to all dentary teeth except the median series of enlarged teeth, which are firmly ankylosed to the bone. In the dry skull of *P. oblectator* (MCZ 180299) the palatine and pterygoid teeth also appear to be hinged because they are detached anterobasally, just as the maxillary and dentary teeth. Palatine and pterygoid dental kinesis was also evident in a juvenile specimen of *P. tritaeniatus* (AMNH 60712). In several specimens my subjective impression was that the anterior maxillary and dentary teeth were more kinetic than were more posterior teeth, especially those immediately anterior to the fangs. The tendency for more kinetic teeth to occur anteriorly in the jaw may make functional sense if these are the first teeth to engage struggling prey.

In *Pseudoxyrhopus, Heteroliodon, "Pararhadinaea" albignaci,* and *Pararhadinaea melanogaster* the extent of posterior deflection permissible in the kinetic teeth seems to be at most about a 20–30° arc, which is insufficient to allow the teeth to lie in a horizontal plane. This is approximately equivalent to or slightly less than the extent of dental kinesis produced by similar manipulation of preserved specimens of *Liophidium torquatum, L. rhodogaster, L. vaillanti,* and several species of *Lycophidion* and *Mehelya* (personal observations of MCZ specimens). The small degree of dental kinesis contrasts with the condition in some other hinge-toothed snakes such as some species of *Liophidium* and *Scaphiodontophis,* in which the teeth can be folded completely to the jaw line (Savitzky, 1981) (as a caveat, the effect of preservational differences on this character is unknown). However, even in *Liophidium* the degree of dental kinesis seems to vary among species. For example, *L. vaillanti* and *L. torquatum* seem to have less kinetic teeth than does *L. rhodogaster* (Savitzky, 1981; personal observations). Even greater variation in tooth kinesis exists between the three previously recognized groups of snakes having hinged teeth (Savitzky, 1981). Such variation in dental kinesis appears to obtain in *Pseudoxyrhopus* as well, with some species having well-developed kinesis and adults of at least one species lacking it entirely.

In overall tooth morphology and degree of specialization the hinged teeth of *Pseudoxyrhopus* appear more similar to those of Group 3 of Savitzky (1981), including the African genera *Lycophidion* and *Mehelya,* than to those of Group 2, including *Liophidium* (Madagascar), *Scaphiodontophis* (Central America), and *Sibynophis* (southeast Asia).[6] In general, species of Group 3 are less specialized and their teeth are less kinetic than those of Group 2. Species in Group 2 often have distally compressed, sometimes spatulate, teeth that are attached to the bone via a well-defined, thickened pedicel. In contrast, the teeth of Group 3 are more typical in overall morphology, their hinges appear to be less fully developed, and they do not have distinct pedicels. *Pseudoxyrhopus* fits the general pattern of Group 3. However,

[6] Savitzky's (1981, 1983) groups were intended to imply morphological and functional similarity and not necessarily phylogenetic relationship. He suggested that the genera of Group 2 were probably not closely related, implying independent origins of the tooth specializations within this group. However, he conjectured that *Lycophidion* and *Mehelya* (Group 3) were, in fact, close relatives (see also Bogert, 1940).

the teeth of *Heteroliodon* and *Pararhadinaea melanogaster* have an unusual morphology similar to that of the teeth of Group 2 snakes.

Modified Tooth Replacement

Savitzky (1981) observed that the typical snake pattern of alternate tooth replacement had been modified or abandoned in the other hinge-toothed snakes (see also Leviton, 1964; Morgan, 1973). This may be the case in *Pseudoxyrhopus*; tooth-bearing bones in these species typically have few empty sockets (aside from damaged or deteriorated specimens) and adjacent teeth are similarly kinetic or (in *P. tritaeniatus*) firmly ankylosed. In contrast, in most colubrids sockets that are empty or that have loose replacing teeth roughly alternate with sockets occupied with firmly ankylosed teeth (best assessed with fluid-preserved specimens rather than dry skulls). In *P. ambreensis, P. quinquelineatus,* and *P. sokosoko* a tendency toward alternating teeth was more evident on the posterior half of the maxilla (missing teeth were usually posterior ones), whereas the anterior maxillary teeth were nonalternating. This pattern corresponds to a subjective impression of greater kinesis in the anterior teeth than in the posterior ones and suggests a change of tooth replacement mode within the maxilla. Significantly, even *P. tritaeniatus* appears to show modified tooth replacement even though its teeth do not appear to be hinged in adults (the specimen of *P. microps* examined retained too few teeth to evaluate this character; this snake seems to have died some time before preservation, and most teeth were missing).

The precise nature of the modified tooth replacement observed in *Liophidium, Pseudoxyrhopus,* and related genera is uncertain and needs additional study. Morgan (1973), commenting on tooth replacement in several genera subsequently discovered to have hinged teeth, remarked that *Scaphiodontophis* had "simultaneous" (as contrasted with alternate) tooth replacement, but he saw nothing unusual in the replacement patterns of *Liophidium* or *Sibynophis.* However, he was unaware of the unusual hinge attachment of the teeth in all of these genera subsequently discovered (Savitzky, 1981). Savitzky (1981: 348) interpreted the presence of functional teeth in most sockets in *Liophidium* and other genera as evidence of "abandonment or modification of alternate tooth replacement" in these genera. I have made a similar inference for the genera under study herein. But it seems clear that the story is not so simple. Most species have been studied only as dry skulls, which except in special circumstances do not permit examination of tooth replacement directly.

Savitzky (in litt., 16 November 1998) indicated that the observation of functional teeth in most sockets suggests "not so much that alternate tooth replacement is utterly lost as that the process is much more rapid, since bone of attachment needn't be laid down." That is, the fibrous hinge attaching the teeth, which develops relatively early in replacement teeth (Savitzky, 1981), permits more rapid tooth replacement than seen typically in colubrids. The end result is that most tooth sockets in the hinge-toothed snakes have functional teeth. Regardless of the precise pattern or mechanism of tooth replacement, all the genera under study herein have a high frequency of filled tooth sockets, which I interpret to reflect some modification of the underlying pattern of tooth replacement.

DENTITION AND PREY IN *PSEUDOXYRHOPUS* AND RELATED GENERA, WITH A CRITIQUE OF SPECULATIONS ON THE DIETS OF THESE AND OTHER SNAKES

Several peculiar features of the dentition of *Pseudoxyrhopus, Heteroliodon,* and *Pararhadinaea* are seen in other snakes that feed on skinks and gerrhosaurids. These lizards have well-developed osteoderms underlying the scales that when combined with smooth scales and highly

muscular bodies, pose difficulties for capture by snakes (Parker, 1933; Vitt et al., 1977; Savitzky, 1983; Greene, 1989a). Hinged teeth are the most obvious dietary specialization in snakes for these prey, but other characters observed in these species are also frequently associated with this diet (Parker, 1933; Savitzky, 1983; Greene, 1989a, 1997). These characters include (1) the enlarged median series of dentary teeth and/or the dentary diastema observed in *Pseudoxyrhopus, "Pararhadinaea" albignaci,* and *Heteroliodon* and (2) enlarged median maxillary teeth and an exceptionally broad maxillary diastema separating enlarged maxillary teeth in *"Pararhadinaea" albignaci.*

No dietary data are available for these snakes except *Pseudoxyrhopus,* for which two food records are available in addition to the *Amphiglossus melanopleura* eggs reported for *P. oblectator.* Raxworthy and Nussbaum (1994) reported a specimen of *P. kely* (UMMZ 192022; SVL 130 mm) that contained an adult *A. melanopleura.* The intestine of an adult *P. tritaeniatus* (MCZ 182480; SVL 782 mm) from the Ranomafana National Park was packed with fine reddish brown hair that probably belonged to a *Nesomys rufus* (Rodentia: Muridae: Nesomyinae). The identity of the prey is inferred from the distinctively colored fur of this rat and the lack of clear alternatives in a reasonably well-known small mammal fauna (James Ryan, G. Kenneth Creighton, and Louise H. Emmons, unpublished mammal checklist for Ranomafana National Park).

Predation on reptile eggs as reported here for *Pseudoxyrhopus oblectator* is uncommon in snakes, but even many snakes considered to be reptile egg specialists consume lizards (for summaries and references, see Roze, 1964; Broadley, 1979; McDiarmid and McCleary, 1993). Conversely, *Hypsiglena torquata,* a small North American colubrid with enlarged but ungrooved rear fangs, eats primarily lizards (>50% of prey items) but also consumes a high proportion (23%) of squamate eggs (Rodríguez-Robles et al., 1999). The posterior maxillary teeth of snakes that primarily eat reptile eggs are usually laterally compressed and often described as lancet shaped, lanceolate, or bladelike (e.g., Tweedie, 1953; Roze, 1964; Broadley, 1980). These teeth are apparently used to slit the egg shells during ingestion (Roze, 1964).

Harry W. Greene (in litt.) informed me that some observations indicate that reptile eggs may be difficult for snakes to digest without first slitting the shells. Prompted by this idea, I reexamined the three remaining intact eggs removed from *P. oblectator* and, indeed, all three have one or two small slits in them that were undoubtedly made by the snake. Thus, the posterior fangs in some *Pseudoxyrhopus* (and perhaps other members of the *Pseudoxyrhopus* group) may play a more important role in egg predation (if this is frequent) than in subduing active prey. Enlarged posterior fangs are not critical adjuncts to hinged teeth in predation on hardbodied lizards, as is clearly shown by the fact that all other colubrids with hinged teeth have nonenlarged or only slightly enlarged rear teeth. Interestingly, the African hinge-toothed snake *Chamaelycus fasciatus* is also known to eat both lizard eggs and gerrhosaurids (see footnote 4). However, in this species the posterior maxillary teeth are not enlarged, whereas one or two teeth in the middle of the maxilla are enlarged and followed by a broad diastema (Parker, 1933; personal observations).

Raxworthy and Nussbaum (1994) speculated that three species of *Pseudoxyrhopus* (*P. heterurus, P. microps,* and *P. tritaeniatus*) might feed upon stream dwelling frogs of the genus *Mantidactylus* (Ranidae). This inference, based solely on the frequent occurrence of these snakes near streams, is unfounded; snake diets are not easily inferred from macrohabitat associations alone. *Pseudoxyrhopus tritaeniatus,* at least, is frequently found well away from streams (personal observations) and, based

on a single observation, adults feed on mammals. Neither dietary data nor morphological characters suggest that any species of *Pseudoxyrhopus* feed upon frogs.

Although it might be assumed that speculations about snake diets, such as frogs in the diet of *Pseudoxyrhopus,* are harmless, they can thwart attempts to understand the evolution of prey preferences and behavior. Such speculations tend to be picked up in the literature and become repeated so that they take on an aura of truth, despite the weak basis for the original statement. In the case of *Pseudoxyrhopus* diets, Raxworthy and Nussbaum's (1994) original speculation has already been applied to another species of *Pseudoxyrhopus*: "most likely it [*Liopholidophis infrasignatus*] is the main predator (together with *L. epistibes, L. rhadinaea* and *Pseudoxyrhopus sokosoko*) of many *Mantidactylus* species" (Andreone and Randriamahazo, 1997: 120). Andreone and Randriamahazo's inference was not based on new data but apparently on the assumption that Raxworthy and Nussbaum's original statement applied to other species of *Pseudoxyrhopus*; this assumption itself may or may not be a reasonable one because dietary preferences can show interspecific or geographic variation.

Moreover, Andreone and Randriamahazo (1997) provided no data to support their statement that *Liopholidophis infrasignatus, L. epistibes,* and *L. rhadinaea* are "most likely the main predators" of *Mantidactylus* species. The only documented prey records for these snakes are microhylid frogs (*Plethodontohyla* and *Platypelis* spp.) or their eggs in the diets of all three species and a small chamaeleon (*Chamaeleo nasutus*) in *L. infrasignatus* (Cadle, 1996a). Of the other species of *Liopholidophis,* Cadle (1996a) found only one *Mantidactylus* (in *L. lateralis*), whereas other nonmicrohylid dietary records were *Boophis* (Rhacophoridae), *Ptychadena* (Ranidae), and *Heterixalus* (Hyperoliidae). All of these dietary records are from the Ranomafana National Park, where *Mantidactylus* species are abundant. The prevalence of microhylids in diets of most species of *Liopholidophis* for which documentation exists (Cadle, 1996a) is highly interesting from both evolutionary and ecological viewpoints. It invites comparative analyses of snake behaviors, foraging strategies, seasonal dietary variation, and chemosensory capabilities and perhaps even of the defensive mechanisms of Malagasy frogs. Unfounded assumptions about the dietary habits of these snakes misdirect and mislead efforts to understand these interesting natural history phenomena.

Unfounded speculations about snake diets are frequent in the literature, but the determinants of snake dietary preferences are poorly understood. Diet is clearly related only in a very loose and unpredictable way to habitat preferences and prey abundance (Cadle and Greene, 1993). Progress in understanding those determinants will come from more conscientious attention to good natural history observations and knowing when speculations can be reliably extended beyond the hard facts. This attention entails, in the present case, the realization that snake diets and macrohabitats are connected only in the loosest possible way and that reliable dietary inferences cannot be made on that basis alone.

My speculation on the diets of *Pseudoxyrhopus* are rooted in known dietary variation for these species and on morphological attributes known to be associated in colubrids with particular dietary spectra. The presence of a diastema in the dentary tooth row in at least five species of *Pseudoxyrhopus* (including *P. tritaeniatus, P. kely,* and *P. microps*; Table 2), the presence of hinged teeth in most species of *Pseudoxyrhopus,* and the enlarged median series of dentary teeth are characters often associated in snakes with a diet of hard-bodied lizards such as skinks and gerrhosaurids (Savitzky, 1983; Greene, 1989a; see also footnote 4). These morphological characters strongly suggest that these lizards are common prey for species of *Pseu-*

doxyrhopus. Unless contradictory observations are forthcoming, the dentitional morphology and definite diet records make it unlikely that any species of *Pseudoxyrhopus* feed on frogs, contrary to Raxworthy and Nussbaum (1994) and Andreone and Randriamahazo (1997).

These inferences concerning diet would seem to be contradicted by the observation of mammal remains in the gut of an adult *Pseudoxyrhopus tritaeniatus.* However, this snake is one of three large species of *Pseudoxyrhopus* (adult SVLs > 800 mm; the other species attaining this size are *P. ankafinaensis* and *P. microps*). A common ontogenetic dietary shift seen in many species of colubrids is from a juvenile diet of lizards to an adult diet of mammals (e.g., Greene, 1989b), but it occurs only in those species attaining large body size or having special means of dealing with mammalian prey (for discussion, see Cadle and Greene, 1993). The shift seems to occur most often around a body size of 500 mm SVL (unpublished observations; also, see Greene, 1989b, fig. 1), although other factors such as body mass, venom capability, and/or constricting ability are also important (venoms and constriction are unknown in *Pseudoxyrhopus*). Accordingly, only the three large species of *Pseudoxyrhopus* routinely attain sufficient size and may show this dietary shift, although exceptionally large individuals of *P. heterurus* attain just over 500 mm SVL (Raxworthy and Nussbaum, 1994) and may also fit the pattern. Other species of *Pseudoxyrhopus* are smaller.

Intriguingly, the switch from hinged juvenile teeth in *P. tritaeniatus* to firmly ankylosed adult teeth may correlate with the suggested ontogenetic dietary shift; firmly ankylosed teeth would probably be critical in subduing struggling mammalian prey. Unfortunately, sample sizes are far too small to confirm this suspected ontogenetic shift or to examine other parameters relevant to the natural history of *Pseudoxyrhopus,* such as frequency of prey use and predator/prey mass ratios (Greene, 1983, 1989b). If confirmed, a shift from hinged to firmly ankylosed teeth in *P. tritaeniatus* correlated with an ontogenetic dietary shift would be the first instance in colubrids in which a dietary change entails a concomitant change in a specific morphological character associated with prey acquisition.

The configuration of the maxillary and dentary dentition in *Pseudoxyrhopus* is probably associated with a fundamental dietary repertoire of skinks and gerrhosaurids. However, some inter- and intraspecific variation in dental characters does occur, such as the interspecific differences in overall tooth form. Other types of dental variation occur in the related taxa *Heteroliodon, Pararhadinaea melanogaster,* and *"Pararhadinaea" albignaci.* The existence of such variation among species that share fundamental and unusual dental characteristics might imply differing degrees of morphological specialization or perhaps different prey types or dietary spectra. Based on a single observation for *Pseudoxyrhopus oblectator,* the biological role of the posterior fangs of these snakes may be associated with predation on reptile eggs rather than on active prey, although a role in both behaviors is possible (knowledge of venoms would aid in interpreting this character). The enlarged dentary teeth and the dentary diastema (possibly variable in *Pseudoxyrhopus oblectator*) appear universally among species of *Pseudoxyrhopus.* Hinged teeth are also present universally in the species examined, but the ontogenetic trend to fully ankylosed teeth observed in *P. tritaeniatus* may be characteristic of those species attaining large body sizes and perhaps switching to different (mammalian) prey.

Similar interspecific variation has been reported for some other colubrid genera. For example, Savitzky (1981) reported variation in tooth form, extent of fang enlargement, and degree of tooth hinging among species of *Liophidium.* This example is germane to the present discussion because *Liophidium* shares several unusu-

al dental characters with *Pseudoxyrhopus, Heteroliodon, Pararhadinaea melanogaster,* and *"Pararhadinaea" albignaci. Liophidium,* in addition, is also known to prey largely, if not exclusively, upon skinks and gerrhosaurids (Savitzky, 1981).[7] Because all recorded activity patterns for species of *Pseudoxyrhopus* suggest exclusive nocturnality (Raxworthy and Nussbaum, 1994; personal observations), whereas potential skink and gerrhosaurid prey are all diurnal, *Pseudoxyrhopus* probably forages differently than do species of *Liophidium,* which are also diurnal (personal observations). This assumes, of course, that skinks and gerrhosaurids are the primary prey of *Pseudoxyrhopus,* which seems likely based on known diets and morphological variation.

DENTITION OF *PARARHADINAEA MELANOGASTER* BOETTGER

Background

Based on new data and clarifications presented herein I reconsider the relationships of *Pseudoxyrhopus* and offer an alternative to the hypothesis presented by Raxworthy and Nussbaum (1994). However, published descriptions of dentitional characters for the other Malagasy genera presumed to be close relatives of *Pseudoxyrhopus, Pararhadinaea* and *Heteroliodon,* need to be corrected and augmented. *Pararhadinaea* currently has three named forms: *Pararhadinaea melanogaster* Boettger (1898) (type species), *P. albignaci* Domergue (1984), and *P. melanogaster marojejyensis* Domergue (1984). *Heteroliodon* is monotypic: *Heteroliodon occipitalis* (Boulenger, 1896).

Pararhadinaea, Heteroliodon, and *Pseudoxyrhopus* historically have been distinguished in part on the basis of maxillary and dentary dentition (e.g., Guibé, 1958; Raxworthy and Nussbaum, 1994). For example, the absence of a maxillary diastema in *Pararhadinaea* was used to distinguish that genus, known at the time only from *P. melanogaster* Boettger, from *Pseudoxyrhopus* (Guibé, 1958). However, this character varies within *Pseudoxyrhopus.* More importantly, the maxillary and dentary dentitions of *"Pararhadinaea" albignaci* and of *Pararhadinaea melanogaster* are morphologically very dissimilar. The dentition of neither species has been accurately described apart from Boettger's (1898) incomplete description for *P. melanogaster.* Thus, despite the strong differences between these species, some dentitional characters of *"Pararhadinaea" albignaci* have been assumed to apply to *P. melanogaster* (type species of *Pararhadinaea*) and have been used in diagnoses and descriptions of *Pararhadinaea* (Raxworthy and Nussbaum, 1994). In addition, *"Pararhadinaea" albignaci* has a dentition that is unique among the genera under consideration (and unusual among colubrids generally); no one has previously called attention to these unique characteristics. The confusion has resulted in the erroneous attribution of some characters to *Pararhadinaea* and failure to appreciate dentitional diversity in these snakes. Similarly, Raxworthy and Nussbaum (1994) inaccurately described the dentition of *Heteroliodon* and failed to note some of its unusual characters.

Because proper attribution of characters and accurate descriptions are germane to the phylogenetic hypotheses for these snakes, I first unravel the confusion created by the most recent review (Raxworthy and Nussbaum, 1994) and then augment previously published descriptions. Because

[7] To Savitzky's (1981) data can be added the following. The stomach of MCZ 180381 (*Liophidium rhodogaster*; SVL 169 mm, 2 g in life) contained two pieces of broken tail from the skink *Amphiglossus melanopleura.* The tail pieces showed essentially no evidence of digestion, indicating recent ingestion; the snake was captured at 1345 h and thus was foraging during the day. Most likely, the skink was grabbed by the tail and escaped, leaving the snake with the autotomized portions of the tail. A specimen of *Liophidium torquatum* (BMNH 89.4.11.10.15; SVL 454 mm, 52 g preserved) contained in its stomach an intact *Zonosaurus madagascariensis* (Gerrhosauridae) (SVL 47 mm, 2.5 g preserved), swallowed tail first.

the dental differences between *Pararhadinaea melanogaster* Boettger (type species) and *"Pararhadinaea" albignaci* Domergue bear on proper diagnosis of *Pararhadinaea* and on the generic allocation of *"Pararhadinaea" albignaci,* I begin with a redescription of the dentition of the holotype of *P. melanogaster.* Descriptions of the dentition of *"Pararhadinaea" albignaci* and *Heteroliodon occipitalis* follow.

Redescription of the Dentition of *Pararhadinaea melanogaster* Boettger (Fig. 7)

Boettger's (1898: 33) description of the dentition of the holotype of *Pararhadinaea melanogaster* (SMF 17885) is essentially correct (my translation):

> —Upper jaw [Maxilla] delicate and slender, with about 17 delicate, equally spaced teeth that gradually increase in length toward the back, only the rear-most measurably enlarged, compressed. Lower jaw broad, robust, with 11 rather blunt teeth, the anterior [ones] small, gradually becoming larger toward the back; from the sixth considerably larger and broadly supported.

Additional details reported here are based on my study of the holotype (Fig. 7). Both maxillae (+anterior tip of each ectopterygoid) and the right dentary (+anterior tip of compound bone) had been previously dissected from the specimen, probably by Boettger, and are in an associated vial.

Maxillary teeth 14+2 (left) and 13+2 (right), the last two teeth enlarged and ungrooved (inferred from the tooth socket size and the posterior fang on the left side, which although loose is the only fang still in place). No diastema separating the fangs from the anterior teeth. Anterior maxillary teeth gradually increase in size anterior to posterior, and the most posterior tooth of this series is only slightly smaller than the fangs (Fig. 7).

Dentary teeth 12, gradually increasing in size from the first to the sixth. Teeth 7–10 are larger and more robust than the anterior series and are approximately the same size as one another. Tooth 11 is missing but judging from the socket it was slightly smaller than tooth 10. Tooth 12 is much smaller than teeth 7–10. An unusual feature is the exceptionally wide spaces between teeth 7–10 (Fig. 7). The lower jaw itself is also robust, particularly considering the size of this snake (239 mm total length).

Aside from a minor difference in tooth counts and the few additional details noted here, my assessment of the dentition of *Pararhadinaea melanogaster* is similar to that of Boettger (1898). Boettger noted that the dentary teeth of *P. melanogaster* were "rather blunt." In fact, both maxillary and dentary teeth are somewhat blunt and robust. The maxillary teeth (except for the fangs) and the anterior dentary teeth are slightly compressed anteroposteriorly at their tips and are hinged; they can be deflected with a fine needle. Most tooth sockets are occupied by functional teeth, which suggests that alternate tooth replacement has been modified. Following Boettger (1898), Mocquard (1909: 41) and Guibé (1958) correctly described the general configuration of the maxillary and dentary dentition of *P. melanogaster,* but subsequent accounts have erred in essential details.

The dentary dentition of *Pararhadinaea melanogaster* is different than the characterization of *Pararhadinaea* given by Raxworthy and Nussbaum (1994: 30): "anterior dentary teeth same size as posterior dentary teeth, middle one or two dentary teeth considerably enlarged" (cf. Fig. 7). The error is based on their examination of *"Pararhadinaea" albignaci,* which does have a pair of median enlarged dentary teeth similar to those of *Pseudoxyrhopus* (but different from those of *Pararhadinaea melanogaster*; Fig. 7), and a mistranslation of Boettger's (1898) description of the dentary teeth of *Pararhadinaea melanogaster.* Raxworthy and Nussbaum's (1994: 32) translation ("11 dentary teeth, the sixth considerably enlarged") missed a small but crucial part of Boettger's description (which was correctly quoted by Mocquard

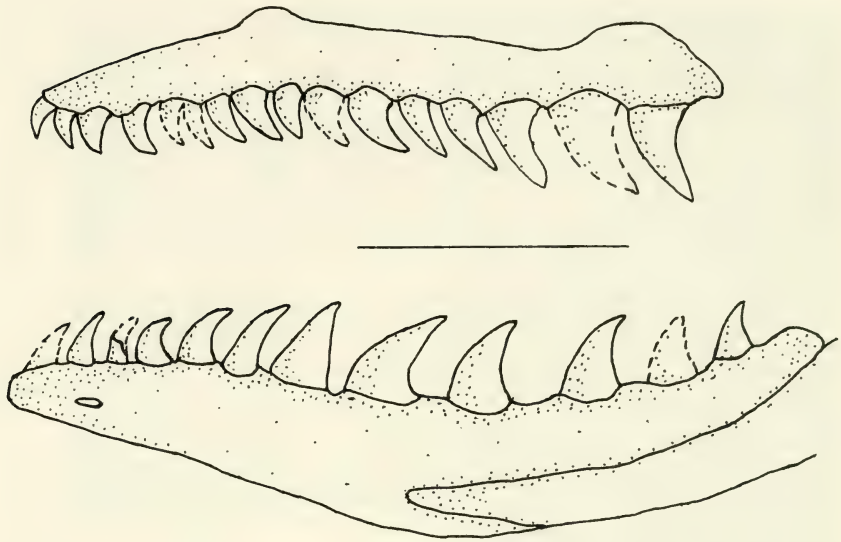

Figure 7. Left maxilla and right dentary (reversed) of *Pararhadinaea melanogaster* Boettger (holotype, SMF 17885). Teeth drawn with dotted lines are missing. As in *Pseudoxyrhopus oblectator* (see Fig. 4), some of the teeth in this specimen were detached anterobasally and folded down; these have been restored to their normal position in the drawing. Scale bar = 1 mm.

[1909] and Guibé [1958]): "11 . . . teeth . . . gradually becoming larger toward the back; *from* the sixth [vom sechsten] considerably larger" (emphasis added). Thus, *Pararhadinaea melanogaster* does not have one or two enlarged dentary teeth, but the entire posterior series after the sixth tooth (except the last tooth) is greatly enlarged (Fig. 7). Apart from mischaracterizing the dentary dentition of *Pararhadinaea melanogaster,* Raxworthy and Nussbaum (1994) overlooked critical aspects of the maxillary dentition of *"Pararhadinaea" albignaci.*

The interpretation of *Pararhadinaea* as having "one or two enlarged median dentary teeth" is problematic because all dentary teeth posterior to the first five or six are enlarged (Fig. 7). One interpretation of this condition is that *Pararhadinaea* has enlarged median dentary teeth (a character homologous with that of *Pseudoxyrhopus, "Pararhadinaea" albignaci,* and *Heteroliodon*) and enlarged posterior dentary teeth. However, the wide spacing of the posterior dentary teeth in *Pararhadinaea melanogaster* is quite different from and possibly not homologous with the condition in the other taxa. This ambiguity has important consequences for understanding the relationships of *Pararhadinaea.*

Aside from the holotype of *Pararhadinaea melanogaster* (Fig. 8), the species is known definitely from only two other specimens, the holotypes of *P. m. marojejyensis* Domergue, 1984 (MNHN 1982-1220; Fig. 9) and *Rhabdotophis subcaudalis* Werner, 1909 (SMNS 4235; see Schlüter and Hallermann, 1997). Boettger (1913: 326) stated that another specimen was in the Naturhistorische Museums in Lübeck, Germany, but its present status is unknown.

The dentitions of the holotypes of *Pararhadinaea m. marojejyensis* and *Rhabdo-*

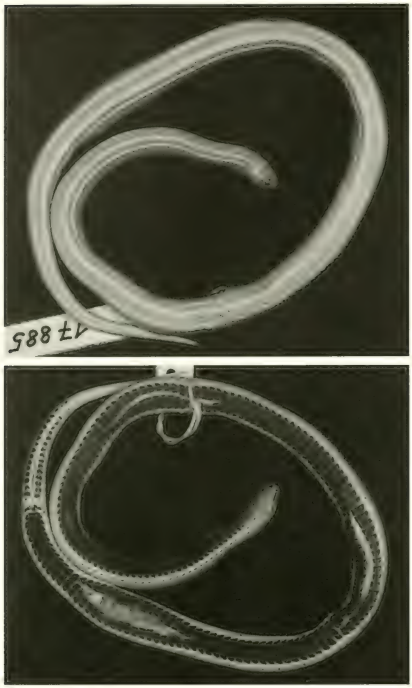

Figure 8. Dorsal and ventral views of the holotype of *Pararhadinaea melanogaster* Boettger (SMF 17885). Total length = 239 mm. Approximately ×1.08.

tophis subcaudalis are identical in configuration to that of the type of *P. melanogaster*. MNHN 1982-1220 and SMNS 4235 have, respectively, 12+2 and 14+2 maxillary teeth on the right side (the left maxilla of SMNS 4235 is missing). As in SMF 17885 the maxillary teeth in both specimens gradually increase in size posteriorly, a diastema is absent, and the fangs are ungrooved and slightly larger than the immediately preceding teeth. In both MNHN 1982-1220 and SMNS 4235 the tooth immediately preceding the first fang is approximately two-thirds the length of the fangs (three quarters of the length in SMF 17885). All maxillary teeth are hinged except for the fangs (and perhaps the last tooth immediately preceding the fangs in MNHN 1982-1220).

SMNS 4235 has 14 dentary teeth on each side. The anterior dentary teeth are small and hinged. Teeth 7–9 are abruptly enlarged (especially teeth 8 and 9), and these are followed by five large, widely spaced teeth similar to those of SMF 17885 (Fig. 7); narrow gaps separate the first nine dentary teeth. Apart from the first six teeth, none of the dentary teeth are hinged. In MNHN 1982-1220 the anterior six dentary teeth are small and hinged, and these are followed by five or more enlarged, firmly ankylosed, widely spaced teeth (the posterior dentary teeth of this specimen were not thoroughly investigated).

A Comparison of the Known Specimens of *Pararhadinaea melanogaster* Boettger

The three known specimens of *Pararhadinaea melanogaster* have never been directly compared and some comment on their characters seems warranted. The provenance of the type of *Rhabdotophis subcaudalis* is unspecific (type locality: "Madagascar"), whereas the other two specimens are from two widely separated localities in northern Madagascar: Nosy Be, an island off the northwest coast (type of *P. melanogaster*) and the Marojejy region of northeastern Madagascar (type of *P. m. marojejyensis*). Domergue's (1984: 152) statement of the type locality for *P. m. marojejyensis* ("Forêt du massif montagneux du Marojejy") implies that the snake was collected in the high mountains of the Marojejy region, which attain elevations greater than 2,000 m; this has been the interpretation of other authors (e.g., Glaw and Vences, 1994). However, Charles P. Blanc, who collected the specimen during a survey of the Marojejy region in the early 1970s, informed me that the snake was collected near sea level on the coast. Thus, it was probably collected outside the present limits of the Reserve Naturelle Integrale de Marojejy, whose

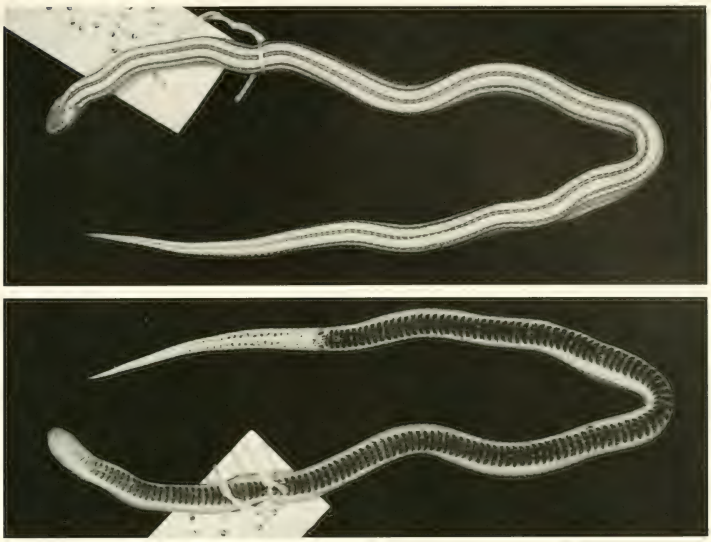

Figure 9. Dorsal and ventral views of the holotype of *Pararhadinaea melanogaster marojejyensis* Domergue (MNHN 1982–1220). Total length = 185 mm. Approximately ×1.14.

eastern boundary lies some 40 km from the coast (Nicoll and Langrand, 1989). (For additional details about the circumstances of capture of this specimen, see the later discussion of character 11.)

A summary of standard systematic characters for the three specimens of *Pararhadinaea melanogaster* is given in Table 3. Apart from a markedly lower ventral scale count in MNHN 1982-1220, all characters are essentially the same in the three specimens. The low ventral scale count of MNHN 1982-1220 as compared with the type of *P. melanogaster* was Domergue's (1984) primary reason for naming that specimen as a subspecies of *P. melanogaster*; however, in the absence of knowledge of populational variation the distinction seems pointless.

The three specimens differ somewhat in color pattern (colors in life are unknown). MNHN 1982-1220 and SMNS 4235 have more irregular markings than does SMF 17885, and the width of the stripes varies among the specimens. In SMF 17885 the stripes are centered at midbody on row 3 (plus half of the adjacent rows), on the suture between rows 5 and 6 (covering half of each row), and on row 9 (plus half of the adjacent rows). In MNHN 1982-1220 the lateral stripe is slightly broader (row 3 + two-thirds of the adjacent rows) and the vertebral stripe is slightly narrower (row 9 + one-third of the adjacent rows). In SMNS 4235 the lateral stripe is still broader (rows 2 and 3 + lower half of row 4 and upper edge of row 1), whereas the dorsolateral and vertebral stripes are about the same as in MNHN 1982-1220. Additionally, in SMNH 4235 dorsal row 1 is heavily and irregularly speckled with dark pigment, making the lateral stripe appear even broader.

The proper taxonomic allocation of *Rhabdotophis subcaudalis* has been in dispute. After describing *R. subcaudalis* in

TABLE 3. SCALE COUNTS, MEASUREMENTS, AND OTHER DATA FOR THE THREE KNOWN SPECIMENS OF *PARARHADINAEA MELANOGASTER* BOETTGER. BILATERAL COUNTS (E.G., HEAD SCALES AND POSTERIOR SCALE REDUCTION) ARE GIVEN FIRST FOR THE LEFT SIDE, THEN FOR THE RIGHT.

	SMF 17885 (holotype)	MNHN 1982-1220 (holotype of *P. m. marojejyensis* Domergue (1984))	SMNS 4235 (holotype of *Rhabdotophis subcaudalis* Werner (1909))
Sex	female	female	male
Total length (SVL[1]) (mm)	239 (201)	185 (152)	212 (182)
Tail length (mm)	38	33	30
Tail length/total length	0.16	0.18	0.14
Maxillary teeth	14+2 13+2	12+2	14+2
Dorsal scales	17-17-17	17-17-17	17-17-17
Ventral scales	163	145	168
Subcaudal scales	40	41	37
Anal scale	divided	divided	divided
Preocular scales	1, 1	1, 1	1, 1
Postocular scales	2, 2	2, 2	2, 2
Temporal scales			
Anterior	1, 1	1,1	1, 1
Posterior	2, 2	2, 2	2, 2
Supralabial scales (touching eye)	7, 7 (3+4)	7, 7 (3+4)	7, 7 (3+4)
Infralabiale scales	8, ?	8, 9	8, 8

[1]SVL = snout–vent length.

1909, Werner synonymized it with *Pararhadinaea melanogaster* Boettger (Werner, 1929). The synonymy did not originate with Guibé (1958), as thought by Brygoo (1983) and Raxworthy and Nussbaum (1994), who nevertheless followed Werner and Guibé in this regard. However, Boulenger (1915) synonymized *Rhabdotophis* with *Pseudoxyrhopus* and recognized *subcaudalis* as a valid species of *Pseudoxyrhopus,* at the same time maintaining the validity of *Pararhadinaea melanogaster.* My comparison of the types of *R. subcaudalis* and *P. melanogaster* conclusively show that both names refer to the same taxon, *Pararhadinaea melanogaster.*

Several characteristics of *Rhabdotophis subcaudalis,* as described by Werner (1909), are not quite accurate and may account for some of the confusion about the proper allocation of the name. For example, Werner (1909: 58) described (in part) the dentition and color pattern of *Rhabdotophis* as follows (my translation):

> —Upper jaw [maxillary] teeth gradually increasing in size from front to back (about 10–12), the last very robust, conical, and slightly curved, not separated from the preceding by an interspace. The front lower jaw [dentary] teeth somewhat elongated. . . . A dark postocular stripe running along the flanks in a longitudinal band over 3½ scales wide.

As indicated in the descriptions of dentition for *Pararhadinaea melanogaster,* Werner (1909) miscounted the maxillary teeth (SMNS 4235 has 16 total maxillary teeth), and rather than having somewhat elongated anterior dentary teeth, the dentary teeth of SMNS 4235 are like those of *P. melanogaster,* in which the anterior six dentary teeth are actually smaller than any other teeth in the lower jaw. Werner's description of the anterior dentary teeth of *R. subcaudalis* as "somewhat elongated" implies that they were longer than more posterior teeth, a condition that more closely approximates the condition in some species of *Pseudoxyrhopus* (see Fig. 6). This may be the reason Boulenger (1915) synonymized the two genera. Additionally, although the lateral stripe in SMNS 4235 is broader than that in the other two spec-

imens (but not fully 3.5 scales wide), all three specimens of *P. melanogaster* differ from one another in the width of the stripes.

DENTITION OF "*PARARHADINAEA*" *ALBIGNACI* DOMERGUE AND A NEW GENUS

Subsequent to Guibé's (1958) review, Domergue (1984) described two new forms of *Pararhadinaea, P. melanogaster marojejyensis* and *"Pararhadinaea" albignaci.* Although Domergue did not examine the dentition of *P. m. marojejyensis,* it is similar to that of the nominal form. However, Domergue (1984: 153) described the maxillary dentition of *"Pararhadinaea" albignaci* as follows (my translation): "5 small anterior teeth, subequal, separated by a long interval from a single tooth that appears somewhat more robust." In reviewing the systematics of *Pararhadinaea,* Raxworthy and Nussbaum (1994) only studied material of *"Pararhadinaea" albignaci,* relying on Boettger's and Domergue's descriptions for the other forms. Unfortunately, both the maxillary and dentary dentitions of *"Pararhadinaea" albignaci* are substantially different from those of *P. melanogaster,* type species of *Pararhadinaea.* Moreover, Domergue (1984) and Raxworthy and Nussbaum (1994) failed to notice some highly unusual features of the dentition of *"Pararhadinaea" albignaci.* These omissions resulted in an erroneous characterization of both the maxillary and dentary dentition of *Pararhadinaea* (see above discussion of *P. melanogaster*) (Raxworthy and Nussbaum, 1994: 29–30):

> posteriormost one or two teeth of maxilla enlarged compared to anterior teeth; anterior dentary teeth same size as posterior dentary teeth, middle one or two dentary teeth considerably enlarged . . . [the enlarged posterior maxillary teeth] may be separated from the anterior teeth by a diastema.

The dentition of *Pararhadinaea melanogaster* differs from Raxworthy and Nussbaum's (1994) description in several ways. First, reference to a single fang in *Pararhadinaea* undoubtedly resulted from failure to observe empty tooth sockets. The three known specimens of *P. melanogaster* and two specimens of *"Pararhadinaea" albignaci* I examined have two fangs and/or sockets. Second, although the rear maxillary teeth of *P. melanogaster* are enlarged, they are only marginally enlarged over the next anterior teeth (Fig. 7). This condition differs from that in *"Pararhadinaea" albignaci,* in which the rear fangs are massively enlarged. Third, *P. melanogaster* lacks a maxillary diastema (an exceptionally broad one is present in *"Pararhadinaea" albignaci*). Fourth, in *P. melanogaster* the posterior dentary teeth are much more massive than the anterior dentary teeth (Fig. 7). Fifth, *P. melanogaster* lacks an enlarged median or anterior series of dentary teeth; instead, approximately the posterior half of the dentary series is enlarged (Fig. 7). However, *"Pararhadinaea" albignaci* does have an enlarged median series of dentary teeth.

All previous descriptions of dentition in *Pararhadinaea,* including Boettger's (1898) for *P. melanogaster,* suggest a rather common colubrid maxillary dentition: a series of small, equally spaced teeth that gradually increase in size posteriorly followed by a pair of slightly enlarged fangs. Aside from the shape of the teeth, the maxillary dentition of *P. melanogaster* conforms to this common pattern (Fig. 7). Interspecific variation in the maxillary diastema is suggested by Boettger's characterization of *P. melanogaster* (diastema absent) compared with the descriptions by Domergue and Raxworthy and Nussbaum (1994) for *"Pararhadinaea" albignaci* (diastema present). This is, in fact, the case (Figs. 7, 10), but there is much more. The only hint of an unusual feature is Domergue's (1984) vague indication of a "long interval" separating the fang of *"Pararhadinaea" albignaci* from the five anterior teeth. However, Domergue (1984: 156) thought the teeth were simply missing from the interval (rather than the space being edentulous) because the specimen was a roadkill and he thought it had perhaps deteriorated. In

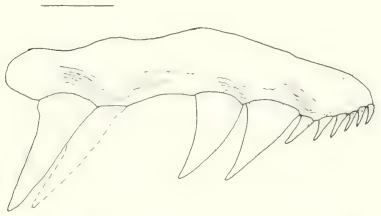

Figure 10. Right maxilla of *"Pararhadinaea" albignaci* (UMMZ 203642) showing the unusual enlarged teeth in the middle of the maxilla followed by an extremely broad diastema. The specimen was drawn from the fluid specimen in situ. Hence, the upper edge of the maxilla as drawn reflects only the soft tissue of the upper jaw and not the dorsal edge of the maxilla. The figure does not adequately portray the strong flexure about the enlarged median teeth, nor the nearly transverse placement of the sockets for the rear fangs (see text). This species is transferred to the new genus *Exallodontophis* herein. Scale bar = 1 mm.

fact, the maxillary and dentary dentition of *"Pararhadinaea" albignaci* Domergue is dramatically different from that of *P. melanogaster.*

I examined the dentition of two specimens of *"Pararhadinaea" albignaci*: MNHN 1982-1221 (holotype) and UMMZ 203642. In the maxilla (Fig. 10) a short anterior series of small teeth is followed by a pair of greatly enlarged teeth (still on the anterior half of the maxilla). A broad diastema and a pair of enlarged, ungrooved rear fangs follow the anterior series. The maxilla itself is rather short and strongly flexed about the point of the enlarged median teeth. Anterior and posterior to this point the maxilla curves strongly medially. The anterior fang on the right side of UMMZ 203642 is missing, but another unusual feature is the nearly transverse alignment of the sockets for the posterior fangs. The posterior fang is strongly offset laterad from the anterior fang. On the left side of this specimen, the two rear fangs are in place and their bases strongly overlap when viewed from the side.

The morphology and dentition of *"Pararhadinaea" albignaci* is highly unusual in having (1) two greatly enlarged teeth at the end of the anterior series of teeth, i.e., in the middle of the maxilla, (2) an exceptionally broad diastema between these enlarged teeth and the ungrooved fangs, and (3) a strong flexure in the middle of the maxilla. In addition, the small teeth anterior to the median enlarged teeth are hinged in the UMMZ specimen of *"Pararhadinaea" albignaci* (I was unaware of the hinged teeth in these snakes in 1994 when I examined the type of *"Pararhadinaea" albignaci* and hence did not check for it). The dentition of *"Pararhadinaea" albignaci* (UMMZ 203642; Fig. 10) is typical: 8+2 maxillary teeth. Teeth 1–6 are small, somewhat kinetic, and gradually increase in size. Teeth 7 and 8 are massively enlarged and akinetic; these enlarged teeth are positioned at a level slightly anterior to the eye underneath the third supralabial and just anterior to the approximate midpoint of the maxilla. The diastema between the eighth tooth and the first fang is equivalent to about one-third the length of the maxillary tooth row, i.e., from the anterior tooth to the anterior edge of the first fang. All teeth in *"Pararhadinaea" albignaci,* including the small anterior series, are rather stout and bluntly pointed. In addition, the enlarged teeth are proportionally much larger in relation to the overall size of the maxilla and other maxillary teeth than is typical for colubrids (cf. Fig. 10 and Figs. 6, 7, 12, 16). The maxillary dentition of the holotype is morphologically similar to that of UMMZ 203642 except that only six teeth are present anterior to the diastema (as reported also for UMMZ 200064 by Raxworthy and Nussbaum, 1994).

The dentary dentition of *"Pararhadinaea" albignaci* (UMMZ 203642) consists of a series of four small anterior teeth that gradually increase in size, a somewhat abruptly enlarged fifth tooth, and two massively enlarged teeth (teeth 6 and 7). The enlarged teeth are followed by a short diastema (approximately equivalent to or slightly less than the base of the following tooth). Because thorough study of the posterior dentary dentition requires destructive manipulation of specimens I did not

examine the posterior dentary dentition further. The first three anterior dentary teeth are smaller than the posterior teeth, whereas the fourth and fifth are subequal to the posterior teeth.

The maxilla and maxillary dentition of *"Pararhadinaea" albignaci* differ from those of *P. melanogaster* (cf. Figs. 7 and 10) in having (1) fewer teeth (6–8+2 vs. 12–14+2), (2) a pair of greatly enlarged teeth in the middle of the maxillary tooth row (absent in *P. melanogaster*), (3) an exceptionally broad diastema between the median enlarged teeth and the posterior fangs (absent in *P. melanogaster*), and (4) a shortened, robust, and strongly flexed maxilla (longer, gracile, and relatively straight in *P. melanogaster*). The maxillary dentition of *"Pararhadinaea" albignaci* is also very different from that of *Pseudoxyrhopus* (Fig. 6) and *Heteroliodon* (Fig. 12), but *Pseudoxyrhopus* and *"Pararhadinaea" albignaci* have a dentary diastema, an unusual character for colubrids.

The strong divergence in maxillary dentition between *"Pararhadinaea" albignaci* and *P. melanogaster* requires reconsideration of the attribution of *albignaci* to *Pararhadinaea*. Domergue (1984) did not fully justify his generic placement, noting only a few characters of habitus and scalation in his redefinition of *Pararhadinaea* (Domergue, 1984: 155–156). He was perhaps influenced by the fact that *"Pararhadinaea" albignaci* and *P. melanogaster* have black venters (see Figs. 8, 9, 11), a somewhat uncommon character in colubrids. In fact, most of the defining characters given by Domergue (e.g., small size, short head little distinct from the neck, short tail, small eye) typify many small cryptozoic colubrids (Cadle and Greene, 1993), including species of other genera from Madagascar. Others (hypapophyses on posterior trunk vertebrae) characterize a wide array of Afro-Malagasy colubrids. Raxworthy and Nussbaum (1994) used similar characters to diagnose *Pararhadinaea* but failed to realize the substantial divergence in dentition between *"Pararhadinaea" albignaci* and *P. melanogaster*. Thus, their diagnosis of *Pararhadinaea* included dentitional characters ("anterior dentary teeth same size as posterior dentary teeth, middle one or two dentary teeth considerably enlarged"; Raxworthy and Nussbaum, 1994: 30) that do not apply to the type species (see Fig. 7). Moreover, although Raxworthy and Nussbaum (1994) observed a maxillary diastema in *"Pararhadinaea" albignaci* they failed to grasp how unusual its exceptional breadth is for a colubrid and did not comment at all on the highly unusual presence of en-

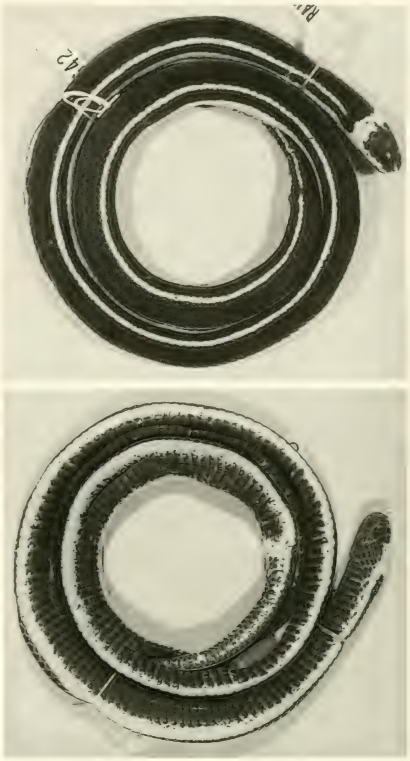

Figure 11. Dorsal and ventral views of *Exallodontophis albignaci* (UMMZ 203642). Total length = 461 mm.

larged teeth in the middle of the maxilla (Fig. 10). In essense, the three nominal taxa currently in *Pararhadinaea* have been placed together on the basis of a suite of characters shared by many small terrestrial and/or cryptozoic colubrids and an erroneous understanding of their dentition.

Because colubrid genera are generally diagnosed in part by sharing basic similarity in the configuration of the dentition (especially on the maxilla), I here transfer *"Pararhadinaea" albignaci* Domergue to a new genus to reflect its substantial dentitional divergence from the type species of *Pararhadinaea, P. melanogaster* Boettger. Of course, one procedure to maintain current nomenclature would be to broaden the diagnosis of *Pararhadinaea* to accommodate a greater diversity of both maxillary and dentary tooth configurations. However, not only would this be counter to usual procedures in colubrid systematics, but evidence adduced below suggests that *"Pararhadinaea" albignaci* is more closely related to *Pseudoxyrhopus* and *Heteroliodon* than to *Pararhadinaea melanogaster.* Maintaining *albignaci* in *Pararhadinaea* would thus render the genus nonmonophyletic.

No generic name is currently available to accommodate *"Pararhadinaea" albignaci,* for which the following new genus is proposed.

Exallodontophis
new genus
Figures 10, 11

Type Species. Pararhadinaea albignaci Domergue, 1984.

Etymology. From the Greek *exallos* (quite different, special, distinguished) + *odontos* (of teeth; from *odous,* tooth) + *ophis* (snake), or "snake of quite different teeth," referring to the unusual maxillary dentition. Gender masculine.

Content. A single species, *Exallodontophis albignaci* (Domergue, 1984).

Definition and Diagnosis. Based on detailed study of UMMZ 203642 and MNHN 1982.1221; augmented with variation reported for *"Pararhadinaea" albignaci* by Raxworthy and Nussbaum (1994). Small, slender terrestrial or cryptozoic colubrids (largest females 415 and 416 mm total length; largest male 291 mm total length). Tail short (11% of total length) and stout. Pupil round. Eye very small, 20% of head depth at midorbit. *Vertebrae:* Hypapophyses present on posterior trunk vertebrae. The hypapophyses are short and with a bluntly pointed posterior projection that barely overlaps the succeeding vertebra. *Dentition:* Maxilla with an anterior series of four to six teeth gradually increasing in size followed by two exceptionally large, ungrooved teeth, a very broad diastema, and two enlarged, ungrooved rear fangs (standard maxillary formula 6–8+2) (Fig. 10). The enlarged median maxillary teeth are immediately anterior to the approximate midpoint of the maxilla; each is about three-quarters of the length of the posterior fangs and at least twice the length and much more massive than any anterior teeth in the maxilla. Dentary with a series of about five teeth that gradually increase in size, followed by a pair of greatly enlarged teeth, a short diastema, and a series of smaller teeth. Maxillary teeth except for the enlarged ones are hinged, but the dentary teeth do not appear to be so. *Scutellation:* Ventrals 180–196. Anal divided. Low number of subcaudals (30–37).[5] Smooth dorsal scales in 17-17-17 rows (no posterior reduction). No apical pits. Supralabials seven, with labials three and four touching the eye. Loreal absent. One small preocular. Infralabials eight. Temporals one + two. *Hemipenis:* "Spinose" (Domergue, 1984), but structural details are unknown.

These traits distinguish *Exallodontophis* from other genera of snakes. The enlarged pair of ungrooved teeth in the middle of the maxilla and the exceptionally broad maxillary diastema are characters distin-

[5] Raxworthy and Nussbaum (1994: 31) reported 10 subcaudal scales in one specimen. This is probably an error or is based on an incomplete tail.

guishing it from all other genera of Malagasy colubrids. The external appearance and configuration of the dentary dentition of *Exallodontophis* are similar to those of *Pseudoxyrhopus,* but species of *Pseudoxyrhopus* have a loreal scale, 19 or more midbody dorsal scale rows that undergo posterior reduction, and longer tails (14–22% of total length). The maxillary and dentary dentition distinguish *Exallodontophis* from the now monotypic *Pararhadinaea. Mimophis* has somewhat enlarged median maxillary teeth (see Bogert, 1940, fig. 15) but lacks a broad maxillary diastema, has grooved rear fangs, and differs in habitus and scutellation from *Exallodontophis.* Some African genera referred to as aparallactines (see Underwood and Kochva, 1993) are superficially similar to *Exallodontophis* and have shortened maxillae with a pair of enlarged teeth situated approximately beneath the eye. However, in these cases the fangs are grooved and are not followed by a diastema and another pair of enlarged teeth.

Distribution. Eastern Madagascar from the vicinity of Perinet (18°56′S, 48°25′E) to Montagne d'Ambre at the northern tip of the island (12°32′S, 49°10′E) (after Raxworthy and Nussbaum, 1994, fig. 23). The three known localities are all within or adjacent to protected areas (Analamazaotra Special Reserve, Marojejy Strict Reserve, and Montagne d'Ambre National Park).

Description and Comparison of Dentition. Exallodontophis albignaci is known from few specimens (four were reported by Raxworthy and Nussbaum [1994], and at least one has been obtained since). Apart from the dental characters described here for the first time, standard scutellational characters and natural history were summarized by Domergue (1984) and Raxworthy and Nussbaum (1994). Although no dietary data are available for *Exallodontophis,* the configuration of the maxillary and dentary dentition suggests a diet of skinks or other hard-bodied lizard prey.

I am unaware of other colubrids with a maxillary dentition like that of *Exallodontophis.* However, some colubrids do have enlarged maxillary teeth positioned more or less as in *Exallodontophis* with respect to, for example, the eye. Among these are many of the African genera frequently referred to as aparallactines (e.g., *Amblyodipsas, Aparallactus, Miodon, Macrelaps, Polemon, Xenocalamus*; see generic diagnoses and fig. 18 of Boulenger, 1896: 244–256). *Exallodontophis* differs from these genera in anatomical details. In aparallactines the enlarged teeth are grooved and are separated by a broad diastema from the preceding small teeth (cf. Fig. 10). Moreover, these enlarged teeth in aparallactines are not followed by another pair of fangs, as in *Exallodontophis.* Shortening of the maxillae seems to be correlated with burrowing habits in colubrids, as suggested by Bogert (1940: 84) among others, and both aparallactines and *Exallodontophis* are known to be at least somewhat fossorial (Broadley, 1983; Raxworthy and Nussbaum, 1994). The superficial resemblances between *Exallodontophis* and aparallactines in the form of the maxilla are possibly due to the constraints imposed by fossorial habits. However, the detailed structural differences between them suggests that *Exallodontophis* is unrelated to aparallactines. Parker (1927) discussed a similar case of putative homoplasy between aparallactines and some fossorial Neotropical colubrids (*Apostolepis* and *Elapomorphus*), which are similar to both *Exallodontophis* and (especially) aparallactines in some of the characters just mentioned (see also Underwood and Kochva, 1993).

Some other nonfossorial African colubrids have enlarged teeth in the middle of the maxilla as well as a pair of posterior fangs (e.g., *Psammophis*; see Bogert, 1940, fig. 15). As with aparallactines, the morphological details in these genera are quite distinct from those of *Exallodontophis.* In these genera the maxillae are relatively much longer than those of *Exallodontophis,* the posterior fangs (but not the median enlarged teeth) are grooved, and the

space between the median and posterior enlarged teeth is occupied by additional teeth as well as a diastema. No characters suggest a special relationship between *Exallodontophis* and these African genera.

DENTITION AND HEMIPENIS OF *HETEROLIODON OCCIPITALIS* (BOULENGER)

Dentition

Boettger (1913) did not examine the dentition in his new genus *Heteroliodon*. Guibé (1958: 218) reported "10 to 15 [maxillary] teeth, the last 2 larger and separated from the preceeding by a space. Mandibular teeth subequal." Raxworthy and Nussbaum (1994: 25) described the dentition of *Heteroliodon*:

> without grooves on teeth; two posteriormost teeth of maxilla separated by a small diastema from anterior teeth; one or both posterior maxillary teeth slightly enlarged compared to anterior teeth; anterior dentary teeth same size as posterior dentary teeth, middle (fifth and sixth) dentary teeth considerably enlarged.

I examined the dentition of the holotype of *Heteroliodon occipitalis* (BMNH 1946.1.12.28) and another specimen (BMNH 1930.7.1.238). Some details differ from previous descriptions, and other noteworthy details have not previously been reported. Because the maxillae of BMNH 1930.7.1.238 are relatively undamaged as compared with those of the holotype, most of the description is based on this specimen.

BMNH 1930.7.1.238 has 11+2 maxillary teeth on each side (Fig. 12). No diastema separates the ungrooved fangs from the anterior teeth. The fangs are greatly enlarged (twice or slightly more) compared with the anterior teeth (not slightly enlarged, as reported by Raxworthy and Nussbaum, 1994). Each maxilla has an unusual edentulous extension (no tooth sockets) anterior to the tooth row sufficient to accommodate one or two additional teeth. By contrast, in most colubrids the maxilla is toothed up to and including the anterior tip of the bone (see Figs. 6, 7, 10). All maxillary teeth except the fangs are hinged.

Raxworthy and Nussbaum (1994: 27) claimed that in the holotype of *Heteroliodon occipitalis* the anterior fang was "slightly larger" (left side) or the "same size" (right side) as the anterior teeth (the posterior fang is missing on each side). This asymmetry and the impression of the fangs being no more than slightly larger than the anterior teeth are artifacts: both fangs in the holotype are broken off at their tips (a greater portion broken on the right side than on the left). The intact teeth were undoubtedly much larger than the anterior teeth and symmetric, as in BMNH 1930.7.1.238 (Fig. 12). Raxworthy and Nussbaum (1994: 26) also reported that in UMMZ 197143 the fangs were enlarged "only very slightly," but I suspect either damaged teeth or an erroneous interpretation based on the above observations. The maxillary tooth formulae of the holotype of *Heteroliodon occipitalis* are 10+2 (left) and 11+2 (right). The fangs are greatly enlarged (as in Fig. 12) and separated from the anterior teeth by a space less than one tooth in width (but greater than the gap in BMNH 1930.7.1.238). Both posterior fangs are missing, and the tips of the anterior fangs are broken. As in BMNH 1930.7.1.238, the tips of the maxillae are edentulous and the teeth are blunt.

The left dentary of BMNH 1930.7.1.238 has the following tooth formula: 4(5–6)-7 = 13. The right dentary of this specimen appears pathological; it has seven anterior teeth followed by a large interspace (no sockets) and one additional tooth. Dentary formulae for the holotype (BMNH 1946.1.12.28) are 4(5–6)-8 = 14 (right) and 4(5–7)-8 = 15 (left). No dentary diastema is present in either specimen. The tips of the dentaries are edentulous, just as in the maxillae, but that characteristic is scarcely visible in lateral view (Fig. 12) because of the mesiad curvature of the anterior tip of the bone.

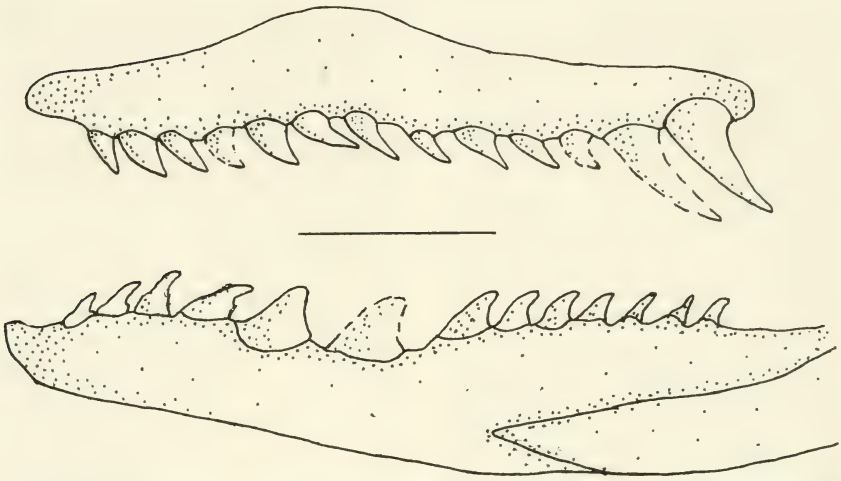

Figure 12. Right maxilla (reversed) and left dentary of *Heteroliodon occipitalis* (BMNH 1930.1.238). Teeth drawn with dotted lines are missing. Note the unusual edentulous anterior portion of the maxilla. Scale bar = 1 mm.

The maxillary teeth in *Heteroliodon* except for the fangs and the dentary teeth except for the median enlarged pair are hinged and have a mobility comparable to species of *Pseudoxyrhopus*.[9] As in *Pseudoxyrhopus,* the anterior teeth in each bone appear more distinctly hinged than the posterior teeth. Individual teeth in *Heteroliodon* are short, blunt, distally slightly expanded in a transverse plane, and anteroposteriorly compressed at the tips. The tooth bases are enlarged, a morphology similar to that of some species of *Liophidium* (see photographs in Savitzky, 1981). There is also a suggestion of a bony pedicel to which the teeth attach, another feature also observed in other hinged-tooth snakes (Savitzky, 1981).

The edentulous tips to the maxillae and dentaries in *Heteroliodon* are unusual and of unknown significance. The maxillae abut posterolateral extensions of the premaxillary bone and are bound to them by strong fibrous tissue; this tissue may play a role in strengthening the snout during burrowing, which is indicated by the few natural observations for this species (Raxworthy and Nussbaum, 1994) and by the similarities to other burrowing snakes in the overall form of the snout and head (see Cadle and Greene, 1993, table 25.1). I am unaware of other snakes in which the anterior end of the maxilla is edentulous except some species in the African genus *Prosymna* (Broadley, 1980: 486). Perhaps only coincidentally, this observation is nevertheless intriguing because *Prosymna* is a specialized predator of reptile eggs (Broadley, 1979, 1980) and one other species of the *Pseudoxyrhopus* group at least occasionally eats reptile eggs. Unfortunate-

[9] The posterior enlarged dentary tooth on the left side of the holotype is loose and might be interpreted as hinged. However, I suspect this loose tooth reflects a stage in normal tooth shedding because the corresponding teeth in BMNH 1930.7.1.238 are firmly ankylosed. The interpretation of the other maxillary and dentary teeth as hinged is based on the fact that all teeth are kinetic, rather than the usual snake condition in which alternate teeth are mobile, reflecting the normal replacement cycle.

ly, no dietary data are available for *Heteroliodon* and whether this unusual character is correlated with such a diet is unknown.

In summary, the dentition of *Heteroliodon* is unusual in the following characters: (1) edentulous tips to the maxilla and the dentary, (2) gap of variable width separating the fangs from anterior maxillary teeth, (3) enlarged median series of dentary teeth, (4) teeth hinged except for the enlarged maxillary and dentary teeth, and (5) unusual overall tooth form.

Hemipenis

The right inverted hemipenis of BMNH 1930.7.1.238 was studied in situ through a previous midventral incision in the tail and a medioventral incision in the ventral lobe of the right hemipenis. The hemipenis extends to the level of the suture between subcaudal scales 7 and 8 (7.5 mm total length) and divides at the level of the suture between subcaudals 4 and 5 (4 mm from the base). Thus, it is approximately 45% bilobed. The sulcus spermaticus divides at the level of the suture between subcaudals 3 and 4 (3 mm from the base) and apparently passes to the tip of the lobes in the dorsolateral wall of the organ (centrolineal in orientation). The base of the organ below the sulcus division has a sparse covering of small spinules or spinulate papillae. At the point of sulcus division on the asulcate side are approximately two rows of relatively large straight spines. Distal from this point the spines first abruptly and then more gradually decrease in size toward the tips of the lobes. The tips of the sulcus spermaticus end in a relatively large nude area on the tips of the lobes. Aside from the nude tips and the apparently nude crotch of the organ, the lobes are entirely spinose (no calyces). No other conspicuous features, such as pockets or nude areas, are present.

The hemipenis of *Heteroliodon* resembles that of *Pseudoxyrhopus oblectator,* including the following characters: (1) relatively enlarged spines at the point of division of the sulcus spermaticus, decreasing distally from that point, (2) basal region sparsely covered with minute spines, (3) crotch of organ nude, and (4) nude tips to the lobes. The nude apical areas appear relatively larger in *Heteroliodon* than in *P. oblectator,* but it is difficult to quantitatively compare inverted and everted organs.

REVISED DIAGNOSES AND COMMENTARY

Raxworthy and Nussbaum (1994: 3, 25, 30) briefly diagnosed *Pseudoxyrhopus, Heteroliodon,* and *Pararhadinaea* (including *Exallodontophis albignaci* within *Pararhadinaea*) using, in part, characters of the dentition and relative eye size. However, the reinterpretation of dentitional characters and taxonomic revisions reported herein require modification of these diagnoses insofar as tooth characters are concerned. In addition, I believe relative eye size is only a proxy for overall body size and cannot be used as a diagnostic generic character.

Raxworthy and Nussbaum's (1994) diagnosis of *Heteroliodon occipitalis* included having anterior and posterior dentary teeth of equal sizes, maxillary fangs only "slightly enlarged," and a "large" eye (0.35 versus <0.3 times head depth). All of these character states were considered different from those in *Pseudoxyrhopus.* Scoring of the relative size of the fangs in *Heteroliodon* was based on a damaged specimen. The fangs of *Heteroliodon* are more than twice the size of the other maxillary teeth (Fig. 12) and are proportionally as large as those of *Pseudoxyrhopus.* Similarly, Raxworthy and Nussbaum stated that in *Pararhadinaea* the anterior and posterior dentary teeth were equal in size and erroneously attributed some other dentitional characters to *Pararhadinaea* that are characteristic only of *Exallodontophis albignaci.* In *Pararhadinaea melanogaster* the posterior dentary teeth are much larger than the anterior ones, whereas in *Exallodontophis albignaci,* upon which Raxworthy and Nussbaum based

their diagnosis of *Pararhadinaea,* the anterior and posterior dentary teeth are more nearly the same size.

Moreover, the relative sizes of the anterior and posterior dentary teeth and relative eye size differ among species of *Pseudoxyrhopus* in a manner that diminishes their utility in distinguishing the genera. In effect, both are apparently related to body size, and the smaller species of *Pseudoxyrhopus* are more nearly like *Heteroliodon* and *Pararhadinaea* in both characters. For example, in *Pseudoxyrhopus oblectator* the anterior and posterior dentary teeth (i.e., those anterior and posterior to the median enlarged series) are about the same size. In *P. ambreensis, P. imerinae, P. kely, P. quinquelineatus,* and *P. sokosoko* the anterior teeth are equal to or only slightly larger than the posterior teeth. The size distinction between the anterior and posterior dentary teeth is most obvious in the large species of *Pseudoxyrhopus, P. microps* and *P. tritaeniatus,* in which the anterior teeth are very elongate (Fig. 6). The general pattern in the dentary teeth, as noted by Boulenger (1890), is an increase in tooth size to the median enlarged series and then an abrupt decrease. However, the size increase in the anterior series may be abrupt, as in *P. tritaeniatus* (Fig. 6), or more gradual, as in *P. imerinae, P. oblectator,* and *P. quinquelineatus.* In *P. quinquelineatus* the anterior and posterior dentary teeth are approximately the same size. In any case, because of size variation within the anterior and posterior series, a qualitative distinction in size between the series is imprecise.

The few data on relative eye diameter (RED; eye diameter divided by head depth) preclude adequate statistical evaluation, but several observations suggest that RED is also size related. My reevaluation of RED in these snakes was prompted by comparison of the adult (RED = 0.3) and juvenile (RED = 0.34) specimens of *Pseudoxyrhopus oblectator.* The juvenile value is indistinguishable from that of *Heteroliodon* (0.35) when measurement error is considered. Other data indicating that RED is related to size include (all data from Raxworthy and Nussbaum [1994] except *Pseudoxrhopus oblectator* and juvenile *P. tritaeniatus*) (1) the species of *Pseudoxyrhopus* with the largest RED (*P. kely, P. sokosoko, P. oblectator;* RED = 0.27–0.34) are among the smaller species; (2) *Heteroliodon* and *Pararhadinaea* have larger REDs (0.29–0.35) but are as small or smaller than the smallest species of *Pseudoxyrhopus* (*Exallodontophis albignaci,* with RED = 0.15–0.2, is an exception to the pattern); (3) juveniles of at least two species of *Pseudoxyrhopus, P. oblectator* (MCZ 181287) and *P. tritaeniatus* (AMNH 60712), have larger REDs (0.34 and 0.42, respectively) than adults (0.30 and 0.26, respectively); and (4) although *Exallodontophis albignaci* clearly has a smaller RED than the other genera, RED within this species also shows an inverse relationship with body size (SVLs of 240 mm, 253 mm, and 370 mm with corresponding REDs of 0.20, 0.19, and 0.15). Thus, *Pararhadinaea, Heteroliodon,* and the small species of *Pseudoxyrhopus* have eye sizes that might be considered typical for their body sizes, and relative eye size is therefore only an approximate proxy for body size.

Taking these observations into consideration, the tooth characters used to diagnose *Pseudoxyrhopus, Heteroliodon,* and *Pararhadinaea* can be restated. After removal of "*Pararhadinaea*" *albignaci* to *Exallodontophis, Pararhadinaea* can be characterized much as done originally by Boettger (1898):

> —Maxillary teeth approximately 14–16, equally spaced (no diastema), gradually increasing in size anterior to posterior, with the last two teeth somewhat enlarged, compressed, and ungrooved. Dentary teeth 12–14 with approximately the last half of the series larger and more robust than the anterior teeth; posterior dentary teeth widely spaced. Overall tooth form unusual: tips blunt and compressed. Teeth hinged.

The most distinctive feature of the dentition of *Heteroliodon* and the most diffi-

cult to explicitly describe is the overall tooth form. Otherwise, its dentition can be briefly characterized:

> —Maxillary teeth 10–11+2. Anterior maxillary teeth subequal followed by two greatly enlarged, ungrooved fangs; fangs preceded or not by a gap less than one tooth in width. Anterior tip of maxilla edentulous. Dentary teeth 13–15; two or three median dentary teeth enlarged. Overall tooth form highly unusual: tips blunt, compressed anteroposteriorly, and distally flared in a transverse plane. Teeth hinged.

Pseudoxyrhopus is the most difficult to characterize because of interspecific variation in tooth form and dentitional morphology. The teeth vary from long and slender in the large species such as *P. tritaeniatus* (Fig. 6) to rather shorter and less pointed as in *P. quinquelineatus* and *P. oblectator*. Nevertheless, the following characterization applies to the dentition of all species of *Pseudoxyrhopus*:

> —Maxillary teeth 12–17+2. Anterior maxillary teeth subequal or slightly larger anteriorly; short diastema present or not, followed by two greatly enlarged, ungrooved fangs. Dentary teeth 15–20, with a median series of two or three enlarged teeth usually followed by a short diastema. Teeth hinged except in adults of some species, including at least *Pseudoxyrhopus tritaeniatus*.

A NEW HYPOTHESIS FOR THE RELATIONSHIPS OF *PSEUDOXYRHOPUS, EXALLODONTOPHIS, HETEROLIODON,* AND *PARARHADINAEA: LIOPHIDIUM* AS A MEMBER OF THE *PSEUDOXYRHOPUS* GROUP

Previous Hypotheses and Characters

Raxworthy and Nussbaum (1994: 34, table 7) tabulated characters shared by *Pseudoxyrhopus, Heteroliodon,* and *Pararhadinaea* (although their tabulations for *Pararhadinaea* were based primarily on *Exallodontophis albignaci*). Only one of their characters linking these genera, the series of enlarged median dentary teeth, is unquestionably derived. However, Raxworthy and Nussbaum possibly erred in scoring this as a character of *Pararhadinaea* because, as clarified above, the state of this character in the type species is ambiguous (Fig. 7), thus making enlarged median dentary teeth a character unambiguously shared only by *Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon* (some other Malagasy genera, e.g., *Dromicodryas, Ithycyphus,* and *Langaha* have enlarged anterior dentary teeth). The other shared characters noted by Raxworthy and Nussbaum (1994, table 7) are highly variable among colubrids (e.g., ungrooved, enlarged maxillary fangs) or variable within *Pseudoxyrhopus* and/or *Heteroliodon,* as shown herein (e.g., maxillary diastema). This study adds two other unquestionably derived characters shared by all four genera: hinged teeth and a modified pattern of tooth replacement. Both are also characteristic of *Liophidium.* A dentary diastema is shared by *Exallodontophis* and *Pseudoxyrhopus.*

Thus, the case that all four genera, *Pseudoxyrhopus, Exallodontophis, Heteroliodon,* and *Pararhadinaea,* form a clade relative to other snakes is not compelling based on present evidence because the only previously identified synapomorphy (enlarged median dentary teeth) unambiguously applies only to the first three genera, and two other apomorphies (hinged teeth and modified tooth replacement) apply to these four genera and to *Liophidium.* A consideration of other characters of these snakes reinforces the ambiguous relationship of *Pararhadinaea* to the other genera. I first reconsider Raxworthy and Nussbaum's (1994) claim of a "significant" morphological gap between these and other Malagasy colubrid genera because it bears on the interpretation of the relationships of the group.

Raxworthy and Nussbaum (1994: 34) speculated that the sister group of *Pseudoxyrhopus–Heteroliodon–Pararhadinaea* would be a non-Malagasy colubrid because of perceived "significant morphological and behavioral differences of [these genera] compared to the other Malagasy genera." These perceived differences were

dentition (ungrooved maxillary teeth), body form (low relative head to neck width, "rounded head profile"), and general habits (nocturnal, terrestrial). However, these features often differ considerably among closely related snakes and even substantially within a genus in some cases. Numerous examples exist, but cases illustrating considerable divergence in some or all of these sorts of features include *Epicrates* (Kluge, 1989), Xenodontini (Myers, 1986), *Sibon* and *Dipsas* (Peters, 1960; Kofron, 1980), and *Rhadinaea–Coniophanes–Pliocercus* (Myers, 1974). Even within *Pseudoxyrhopus* the differences in head shape between *P. imerinae* and *P. quinquelineatus* and the other species is substantial. It is premature to exclude other Malagasy genera as potential sister taxa of *Pseudoxyrhopus–Heteroliodon–Pararhadinaea* on the basis of these superficial characteristics. In any case it is unclear in what context these characters differ "significantly" from other Malagasy colubrids because all are observed elsewhere in those snakes.

Hinged Teeth and Tooth Replacement Pattern as Evidence for a Clade of Malagasy Snakes

The discovery of hinged teeth and a modified pattern of tooth replacement in *Exallodontophis, Heteroliodon,* and *Pararhadinaea* and some ontogenetic stages of all examined species of *Pseudoxyrhopus* makes comparison with *Liophidium* inevitable because these derived characters are observed in many, if not most, species of *Liophidium* (Savitzky, 1981; personal observations). The occurrence of hinged teeth in these genera might be viewed as independent adaptations to a diet of hard-bodied lizard prey. Alternatively, the common possession of clearly derived features such as these could indicate a close relationship of the genera (or parts thereof). These two interpretations are not mutually exclusive. For example, the presence of an enlarged median series of dentary teeth is a possible adaptation associated with feeding mode but also may be a synapomorphy indicating close relationship of *Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon.* Because hinged teeth and modified tooth replacement are patently derived characters shared by a small group of Malagasy colubrids, I accept at face value that these characters originated once in the Malagasy snake fauna and thus are strong evidence that *Liophidium, Pseudoxyrhopus, Exallodontophis, Heteroliodon,* and *Pararhadinaea* comprise a monophyletic clade, which I refer to as the *Pseudoxyrhopus* group.

If we accept the hinged teeth and modified tooth replacement as evidence that *Liophidium* is closely related to the other genera, how should we view the "significant morphological and behavioral differences" between *Liophidium* and the other genera perceived by Raxworthy and Nussbaum (1994)? Although the difference in habitus between the large species of *Pseudoxyrhopus* (*P. tritaeniatus, P. microps, P. ankafinaensis*; all >850 mm SVL) and species of *Liophidium* is impressive, it is perhaps no more so than that between the large and small species of *Pseudoxyrhopus* (six species have maximal SVLs of <400 mm and two others are ≤510 mm; data from Raxworthy and Nussbaum, 1994). The two largest species of *Liophidium, L. therezieni* and *L. vaillanti,* attain SVLs of at least 600 mm and 532 mm, respectively. The largest specimens of five other species of *Liophidium* were 187–454 mm SVL (unpublished observations). Moreover, *Heteroliodon occipitalis* and *Pararhadinaea melanogaster* are among the smallest Malagasy colubrids, and *P. melanogaster* is superficially similar to some species of *Liophidium.*

Similarly, my perception is that the small species of *Pseudoxyrhopus* (e.g., *P. ambreensis, P. sokosoko,* and *P. kely*; maximum SVLs of 180–333 mm) are not so different from some species of *Liophidium* in head shape, body proportions, and general habitus, as a superficial comparison readily shows (Figs. 13–15). Several species of *Lio-*

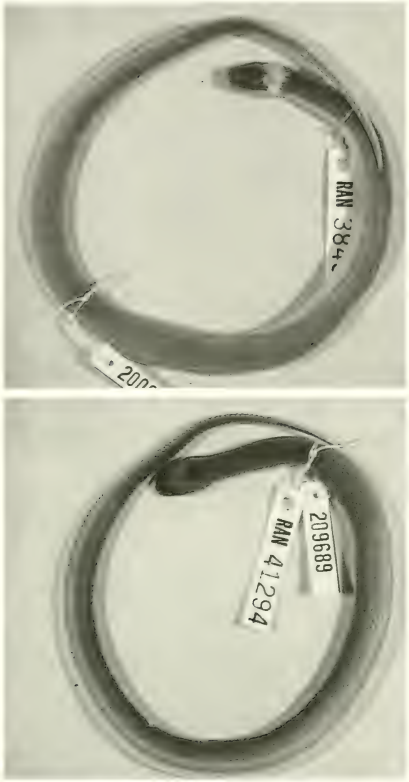

Figure 13. Two small species of *Pseudoxyrhopus*. Both approximately ×0.95. Top: *P. ambreensis* (UMMZ 200062, total length = 344 mm). Bottom: *P. sokosoko* (UMMZ 209689, total length = 323 mm). *Pseudoxyrhopus sokosoko* is one of the species of *Pseudoxyrhopus* lacking a pale nape collar. Both approximately ×0.95.

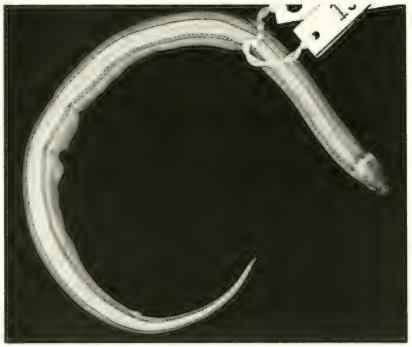

Figure 14. *Pseudoxyrhopus kely* (UMMZ 192022; juvenile male paratype; total length = 184 mm.). This is the smallest species of *Pseudoxyrhopus* (the holotype and only other known specimen is an adult male 217 mm in total length). Approximately ×1.2.

phidium attain body sizes as large or larger than those of some species of *Pseudoxyrhopus* (e.g., *L. vaillanti, L. torquatum, L. therezieni,* and *L. rhodogaster* all attain SVLs of >420 mm). Species of *Pseudoxyrhopus, Exallodontophis, Heteroliodon,* and *Pararhadinaea* have short tails (11–22% of total length), whereas in *Liophidium* relative tail lengths are much more variable (12–27% of total length; personal observations). As in species of *Pseudoxyrhopus, Exallodontophis, Heteroliodon,* and *Pararhadinaea,* the head in *Liophidium* is only slightly distinct from the neck, pupils are round, and the species are terrestrial to cryptozoic (several species of *Pseudoxyrhopus* may be burrowers; Raxworthy and Nussbaum, 1994: 33). The point of these comparisons is not to suggest that these similarities provide evidence of relationship but only that a perception of "significant morphological differences" among these snakes based on superficial characteristics is not especially clear.

Of course, activity patterns do differ among the genera. All species of *Pseudoxyrhopus, Heteroliodon,* and *Exallodontophis* are probably nocturnal, whereas *Pararhadinaea melanogaster* (probably) and species of *Liophidium* are diurnal (personal observations for *Liophidium*; see also footnote 7 and discussion of character 11 for *Pararhadinaea*). This behavioral character was thought by Raxworthy and Nussbaum (1994) to further distance these genera from other Malagasy colubrids.[10] However, divergence in activ-

[10] Raxworthy and Nussbaum (1994) stated that *Par-*

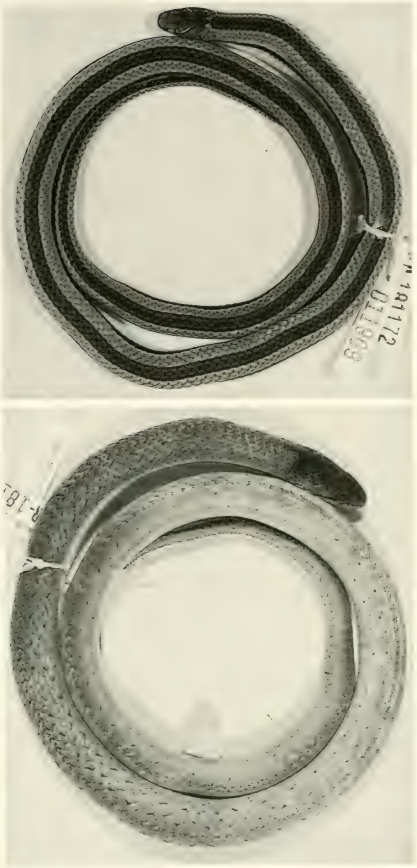

Figure 15. Adults of two of the larger species of *Liophidium*. Top: *Liophidium rhodogaster* (MCZ 181172, total length = 533 mm). Bottom: *Liophidium torquatum* (MCZ 181305, total length = 654 mm).

ity pattern is known to occur among closely related snakes (even varying geographically or seasonally within some species; see Cadle and Greene, 1993). One could even speculate that the divergence in activity pattern between *Liophidium* and the other genera might have been promoted by their presumed strong overlap in dietary resources (see Schoener, 1989, for discussion of divergence in activity pattern as a response to dietary overlap). This divergence would be predicated only on their shared food resource and not on any special evolutionary relationship between the snakes.

In Madagascar, terrestrial to cryptozoic snakes such as *Pseudoxyrhopus* would encounter few other nocturnal snake competitors. Aside from the nocturnal members of the *Pseudoxyrhopus* group and *Madagascarophis* (medium-size to large terrestrial snakes, usually one species per locality), Madagascar's snake fauna is essentially devoid of terrestrial nocturnal snakes (in contrast to arboreal nocturnal snakes of the genera *Geodipsas, Lycodryas,* and *Stenophis*). Nevertheless, it does seem implausible that skinks or gerrhosaurids are such limiting resources as to have effected competition (and therefore temporal divergence in activity) between *Liophidium* and nocturnal species of the *Pseudoxyrhopus* group; these lizards are abundant in areas where the snakes occur. Regardless of the factors responsible for differences in the diel cycles of *Liophidium* and the other genera, this difference alone is insufficient grounds for considering the snakes distantly related.

In conclusion, I see no special morphological disparity between *Pseudoxyrhopus, Heteroliodon, Exallodontophis,* and *Pararhadinaea* and other Malagasy colubrids. I suggest that the hinged teeth and modified tooth replacement provide evidence of a relationship of these snakes with *Liophidium.* Thus, *Liophidium* itself is part of a larger radiation of snakes in Madagascar that manifests a variety of dentitional specializations associated in snakes with feeding on hard-bodied lizard prey: hinged teeth (all genera), enlarged median dentary teeth (*Pseudoxyrhopus, Exallodonto-*

arhadinaea was nocturnal. However, as with their statements concerning dentition for this genus, this behavioral statement is based on observations for *Exallodontophis albignaci. Pararhadinaea melanogaster* is probably diurnal, as indicated by a single observation (see discussion of character 11).

phis, Heteroliodon), diastema in the dentary tooth row (*Pseudoxyrhopus, Exallodontophis*), enlarged median maxillary teeth and broad diastema (*Exallodontophis*), and peculiar tooth form (*Heteroliodon, Pararhadinaea, Liophidium*). The available dietary data, although lacking for most species, are consistent with a shared behavioral repertoire correlated with the morphological characteristics. However, although all of these snakes share the basic dental modification of hinged teeth, the other characters are distributed mosaically among the genera. Thus, if these snakes are a clade exclusive of other Malagasy snakes, the evolution of novel dental and jaw characteristics among them has been quite remarkable.

Comparisons of Other Character Systems in *Liophidium* and the Other Genera

Do other characters offer support for inclusion of *Liophidium* in the *Pseudoxyrhopus* group? Aside from the synapomorphies provided by the dentition, too little is known of other potentially informative character systems to meaningfully compare them. Although hemipenial variation among species of *Pseudoxyrhopus* appears to be minimal, hemipenial variation among species of *Liophidium* is much greater, and some species of *Liophidium* have unusual features such as asymmetry of the hemipenial lobes or basal pockets and lobes (Domergue, 1983; Cadle, 1996a: 392; see also Ziegler et al., 1996).[11] Nevertheless, hemipenes of *Liophidium, Heteroliodon,* and *Pseudoxyrhopus* are similar in being deeply bilobed and entirely spinose, with a centrolineal sulcus spermaticus extending to the tips of the lobes. Domergue's (1983, fig. 5A) illustration of the hemipenis of *L. therezieni* is very similar to that of *P. oblectator* (Fig. 5), and he mentioned (Domergue, 1983: 1117) nude tips to the lobes of the hemipenis of *L. vaillanti* (which I confirmed on MCZ 22203) that seem similar to those I observed in *P. oblectator* and *Heteroliodon occipitalis. Liophidium rhodogaster* also has relatively large nude areas on the tips of the lobes, but these are lacking in *L. torquatum* (personal observations), although *L. torquatum* does have a very tiny patch devoid of spines at the tip of each lobe. Otherwise, the morphology of these hemipenes is very generalized and lacking in clear apomorphies based on present knowledge. The superficial similarity between them may be nothing more than that. Hemipenes of a wide array of African and Malagasy colubrids could be characterized as "bilobed, spinose, and with a centrolineal sulcus spermaticus," but substantive comparisons are presently precluded because detailed descriptions of most taxa are lacking. Unfortunately, hemipenes of *Exallodontophis* and *Pararhadinaea* are unknown apart from Domergue's (1984) uninformative comment that the hemipenis of *Exallodontophis albignaci* was spinose. Nonetheless, the presence of

[11] Ziegler et al. (1996) described the hemipenis of *Liophidium torquatum*, but two of its most unusual characteristics were not mentioned. First, *L. torquatum* (MCZ 181305) has a very deep, elongate nude pocket adjacent to the undivided basal portion of the sulcus spermaticus; it extends from the base of the organ to a level just short of the division of the sulcus spermaticus. The pocket is surrounded by a thickened, somewhat raised border, which is produced into a low lobe on the absulcate edge. Second, the large spines at the base of the hemipenial lobes on the sulcate side of the organ are surmounted on a pair of large globose tuberosities that are clearly set apart from and project above the surrounding tissue of the lobes and base of the hemipenis. Such tuberosities are unknown in other Malagasy snakes. Neither of these features of the hemipenes of *L. torquatum* have been described in other species of *Liophidium* (Domergue, 1983; Ziegler et al., 1996), and they do not occur in *L. rhodogaster* (personal observations of MCZ 181170), whose hemipenis has yet to be described. An unusual characteristic of the hemipenes of several species of *Liophidium* is asymmetry in the length of the lobes. Ziegler et al. (1996) reported slight asymmetry in *L. torquatum*, which I confirmed in MCZ 181305, but the lobes in *L. rhodogaster* (MCZ 181170) are symmetrical. Both *L. torquatum* and *L. rhodogaster* have centrolineal sulci spermatici, which seems to be the case for the species figured by Domergue (1983).

TABLE 4. MAXILLARY DENTITION IN *LIOPHIDIUM*. BILATERAL COUNTS ARE GIVEN WHEN AVAILABLE.

Species/specimens	Tooth count[1]
L. apperti,	
MNHN 1982.442 (type)	24+3
L. chabadi	
MNHN 1978. 2789 (type)	25+2
MNHN 1978.2788	25+3[2]
L. rhodogaster	
MCZ 180381	31+2
MCZ 180382	32+2
MCZ 181169	31+2
MCZ 181170	34+2
MCZ 181171 (Fig. 16)	32+2, 31+2
MCZ 181172	30+2
L. therezieni	
MNHN 1982.444 (type)	27+3
MNHN 1978.1425	30+3
L. torquatum	
BMNH 1946.1.1.38 (type)	29+2
MCZ 180303	28+2
MCZ 181305	25+2
L. trilineatum,	
BMNH 1946.1.15.66 (type)	24+2
L. vaillanti	
MNHN 1901.186 (syntype)	24+3
MNHN 1901.187 (syntype)	23+4
MCZ 22203 (Fig. 16)	21+4, 21+4

[1]No. regular teeth + no. enlarged posterior teeth (which are only slightly enlarged compared with the immediately anterior maxillary teeth) (see Fig. 16).

[2]This count is much greater than the count given by Domergue (1984), who reported 19 total teeth.

the unusual nude apical morphology of the hemipenes of some members of the *Pseudoxyrhopus* group may provide another synapomorphy for this hypothesized clade or parts thereof.

Savitzky (1981) noted that the posteriormost maxillary teeth of *Liophidium rhodogaster* were larger and less effectively hinged than the other teeth. In fact, slight enlargement of posterior maxillary teeth seems to be the rule in *Liophidium*, and two to four posterior teeth may be enlarged (Table 4; Fig. 16).[12] In *Liophidium* these enlarged teeth are only slightly larger than the immediately anterior teeth. They do not approach the size or abrupt enlargement of the rear fangs of *Pseudoxyrhopus, Exallodontophis,* or *Heteroliodon,* which are always much larger than any other maxillary teeth (Figs. 6, 10, 12).

The degree of enlargement of the posterior maxillary teeth varies among species of *Liophidium*. For example, the posterior teeth of *L. vaillanti* are relatively more enlarged than those of *L. aperti, L. chabaudi,* or *L. rhodogaster* (Fig. 16). Although *Liophidium* lacks a maxillary diastema, the holotypes of *L. torquatum* and *L. trilineatum* each have a small gap separating the enlarged teeth from more anterior ones (this character seems to be variable at least in *L. torquatum*; two other specimens lacked such a gap). As noted by Savitzky (1981), the enlarged posterior teeth in *Liophidium* are akinetic or have reduced kinesis as compared with more anterior teeth.

Liophidium and *Pararhadinaea melanogaster* are very similar in the morphology of individual teeth (rather blunt, distally compressed and flared transversely) and in the general morphology of the maxilla and its dentition (teeth gradually increasing in size, with two or more somewhat enlarged posterior teeth, no diastema) (cf. Figs. 7, 16). In contrast, the posterior maxillary teeth in *Exallodontophis, Heteroliodon,*

[12] In *Liophidium* the relative enlargement of the posterior maxillary teeth is subtle and sometimes subjective. For example, Boulenger (1896: 598) recorded three "feebly enlarged" teeth in the type of *L. trilineatum*, whereas I recorded two, and Mocquard (1902) reported that the last "6 or 7" teeth in the syntypes of *L. vaillanti* were "a little longer and more robust" than the others (I recorded three and four enlarged teeth in the two specimens). These discrepancies probably reflect the mainly gradual anterior to posterior enlargement of maxillary teeth in *Liophidium*. The point upon which all authors seem to agree is that some of the posterior teeth in *Liophidium* are enlarged to a variable extent in the different species. This seems to be a somewhat uncommon morphology in colubrids, but it is observed in geographically and taxonomically diverse genera, e.g., the *godmani* group of *Rhadinaea* (Myers, 1974: 28–29) and some species of *Leptophis* (Oliver, 1948: 175–176).

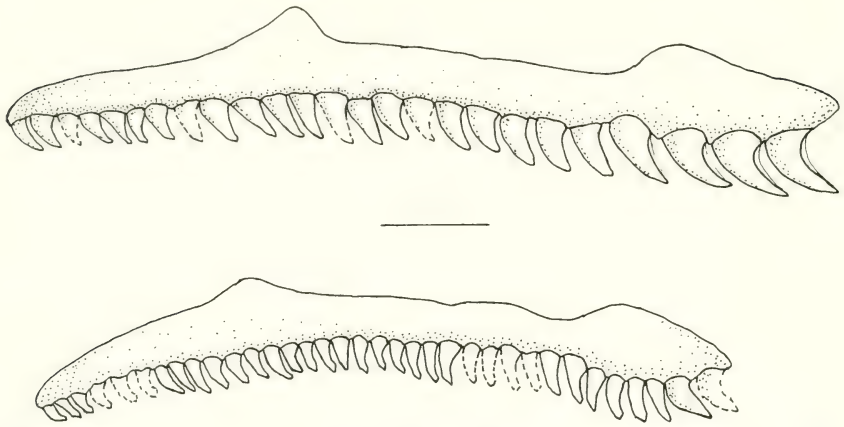

Figure 16. Maxillary dentition of two species of *Liophidium. Teeth drawn with dotted lines are missing. Scale bar = 1 mm. Top: Liophidium vaillanti* (MCZ 22203), left maxilla. Bottom: *Liophidium rhodogaster* (MCZ 181171), left maxilla.

and *Pseudoxyrhopus* are greatly enlarged and often separated by a diastema from the anterior teeth, which usually are subequal or even slightly decrease slightly in size anterior to posterior. The similarities in dentition between *Pararhadinaea* and *Liophidium* account for resolution of these genera as a clade in one of the most parsimonious trees discussed in the next section.

Although I explicitly hypothesize a close relationship of *Liophidium* with *Pseudoxyrhopus, Exallodontophis, Heteroliodon,* and *Pararhadinaea* on the basis of the shared derived characters of hinged teeth and modified tooth replacement, I am not the first to link *Liophidium* with some of these other genera. Mocquard (1909), without stating reasons, postulated that *Pararhadinaea* was "very close" to [*Liophidium*] *vaillanti* (then in the monotypic genus *Idiophis*), noting only that in the former the maxillary teeth increase in size from front to back, whereas in the latter they were subequal (this is more or less true if one ignores the enlarged posterior fangs in *L. vaillanti*; cf. Figs. 7, 16). Mocquard was perhaps impressed with the similarity in maxillary dentition. The dentition of *Liophidium* and *Pararhadinaea* seems to be an uncommon (if not unique) arrangement among Malagasy colubrids. At about the same time Werner (1909) suggested, again for obscure reasons, that his new genus *Rhabdotophis* (=*Pararhadinaea*) was "perhaps closely related to *Pseudoxyrhopus.*" Werner's reasoning is especially obscure because none of the species of *Pseudoxyrhopus* known at the time resemble *Pararhadinaea,* although *Pseudoxyrhopus kely,* discovered much later (Raxworthy and Nussbaum, 1994), is superficially similar in size and color pattern to *Pararhadinaea* (see Figs. 8, 9, 14).

CHARACTER DISTRIBUTIONS IN THE *PSEUDOXYRHOPUS* GROUP

Recognition of *Liophidium* as part of the *Pseudoxyrhopus* group and consideration of the new and corrected morphological data reported herein permits a more detailed analysis of relationships among these snakes than has been attempted before. To estimate the phylogeny of the *Pseudoxyrhopus* group I coded

TABLE 5. DISTRIBUTION OF SELECTED CHARACTERS AMONG *PSEUDOXYRHOPUS*, *EXALLODONTOPHIS*, *HETERO-LIODON*, *PARARHADINAEA*, AND *LIOPHIDIUM*. HYPOTHETICAL ANCESTRAL STATES WERE INFERRED AS DISCUSSED IN THE TEXT FOR EACH CHARACTER. CHARACTER POLARITIES FOR THE INGROUP ARE NOT IMPLIED EXCEPT FOR CHARACTERS IN WHICH THE ANCESTOR WAS CODED AS 0 OR 1. ALTERNATIVE SCORINGS OF SOME CHARACTERS ARE GIVEN IN BRACKETS; UNBRACKETED CODINGS ARE REFERRED TO AS "STANDARD." 01 = POLYMORPHISM, ? = UNCERTAIN.

Character	*Pseudoxyrhopus*	*Exallodontophis*	*Heteroliodon*	*Pararhadinaea*	*Liophidium*	Ancestor
1. Hinged teeth	1 [01]	1	1	1	1	0
2. Tooth replacement	1	1	1	1	1	0
3. Median dentary teeth	1	1	1	0 [1]	0	0
4. Dentary diastema	1 [01]	1	0	0	0	0
5. Maxillary teeth	1	1	1	1	0	?
6. Maxillary fangs	1	1	1	0	0	? [1]
7. Maxillary diastema	01	1	0	0	0	?
8. Head pattern	1	1	1	0	0	0
9. Dorsal scales	1	0	0	0	0 [01]	?
10. Posterior reduction	0	1	1	1	01	?
11. Diel behavior	1	1	1	0 [?]	0	?
12. Body size	01	0	0	0	0	?
13. Tooth form	0	0	1	1	1	0
14. Anterior dentary teeth	0	0	0	1	0	0
15. Number of posterior dentary teeth	01	0	0	0	1	?
16. Number of ventral scales	01	0	0	0	01	?

many of the morphological characters discussed above.

Table 5 shows the distribution of characters used for phylogenetic analysis among the Malagasy snakes with hinged teeth. A few autapomophic characters are included (e.g., character 14) because they have figured prominently in the previous discussions of dentition herein or because my interpretations differ from those given by Raxworthy and Nussbaum (1994). However, other known autapomorphies are not included because they do not contribute to resolution of a phylogeny, although they do aid in diagnosing terminal taxa (e.g., the edentulous anterior extension of the maxilla in *Heteroliodon*). Also, I have ignored characters that do not vary within the ingroup (e.g., absence of grooving on the fangs) even though other character states occur in other Malagasy colubrids.

For some characters more than one scoring was possible depending on how the character was interpreted for particular taxa. These alternatives are indicated in brackets in Table 5. Alternative scorings were included in separate phylogenetic analyses. Three of five alternative scorings (characters 1, 4, 9) were from a single state to polymorphism within a terminal taxon and did not affect the resulting most parsimonious tree topologies but did affect tree lengths and measures of consistency. The other alternative scorings (characters 3, 6, 11) were for alternative states in *Pararhadinaea* and the ancestor.

Characters 1 and 2 provide evidence for the monophyly of the *Pseudoxyrhopus* group (five genera listed in Table 5), defined as the ingroup for the phylogenetic analyses. Because explicit outgroups for this putative clade are as yet unknown, I reconstructed a hypothetical ancestor for purposes of tree rooting. Ancestral states were hypothesized for some characters on the basis of known variation among Malagasy colubrids or colubrids generally. For other characters, ancestral states were not readily apparent and these were coded as unknown (?) in the phylogenetic analyses. The specific rationale for each character is given below. A more detailed discussion of dentition characters (characters 1–7, 13–

15) was given in preceding sections. Character states for *Liophidium* are based in part on unpublished data (see also Domergue, 1983). In the following discussion the state designations 0 and 1 are conveniences with no implication as to which is ancestral or derived, although 0 was assigned to the ancestral state when that could be reasonably inferred.

1. Teeth are firmly ankylosed (0) or hinged (1). All ingroup taxa have hinged teeth. Although adults of *Pseudoxyrhopus tritaeniatus* have firmly ankylosed teeth, juveniles have hinged teeth, as do all other specimens of *Pseudoxyrhopus* examined. Thus, I coded *Pseudoxyrhopus* as state 1, under which the adult condition of *P. tritaeniatus* is interpreted as a reversal, but I also used an alternative coding of polymorphism (01). The ancestor is assumed to have state 0.

2. Tooth replacement is alternate (0) or modified (1). Alternate tooth replacement is the usual condition in colubrids. Tooth replacement in all ingroup taxa is modified. The ancestral condition is assumed to be 0.

3. Dentary teeth are subequal (0) or a median series may be enlarged (1). The condition of *Pararhadinaea* is somewhat ambiguous, and I scored it as 0 and alternatively as 1 for purposes of analysis. In any case, the morphology of the dentary teeth of *Pararhadinaea* is not similar to that of *Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon* (state 1). Alternatively, *Pararhadinaea* could be scored with an autapomorphy for this character, which would not affect tree topologies. The ancestral condition is assumed to be 0.

4. A diastema in the dentary tooth row may be absent (0) or present (1). *Heteroliodon, Pararhadinaea,* and *Liophidium* lack a dentary diastema (0), whereas in *Exallodontophis* a diastema is present (1). Virtually all *Pseudoxyrhopus* examined have a diastema (1) (Table 2); because one specimen lacks a diastema I also used the alternative coding of polymorphic (01). The ancestral condition is assumed to be 0 because dentary diastemata are unknown in other Malagasy colubrids and are otherwise extremely rare in colubrids.

5. Maxillary teeth more than 25 (0) or less than 20 (1). As with any continuously varying quantitative character, discretely coded states are somewhat arbitrary (see Gift and Stevens, 1997, for discussion and references). All species of *Liophidium* have more than 25 teeth (Table 4), whereas no species of the other genera have more than 19 (data presented here and unpublished observations for *Pseudoxyrhopus*). Thus, I arbitrarily coded two states (>25 or <20). Actual ranges are *Pseudoxyrhopus* (14–19),[13] *Exallodontophis* (8–10), *Heteroliodon* (12 or 13), *Pararhadinaea* (13 or 14), *Liophidium* (26–33). The ancestor is coded as unknown (?) because Malagasy colubrids show a broad range of maxillary tooth numbers, which is approximately encompassed by the numbers in the *Pseudoxyrhopus* group (*Exallodontophis* and species of *Liophidium* representing the lower and higher extremes, respectively).

6. Posterior maxillary fangs may be slightly enlarged as compared with the other maxillary teeth (0) or greatly enlarged (1). In *Pararhadinaea* and *Liophidium* the fangs are only slightly enlarged as compared with the immediately preceding teeth (0) (Figs. 7, 16). In *Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon* the fangs are greatly enlarged as compared with the immediately preceding maxillary teeth (1) (Figs. 6, 10, 12) (the greatly enlarged median maxillary teeth of *Exallodontophis* are ignored in scoring this char-

[13] Raxworthy and Nussbaum (1994: 3) reported a range of 9–18 maxillary teeth in *Pseudoxyrhopus.* The lower value was apparently based on the holotype of *P. kely,* which I did not examine (the total count is at least 10 because they missed one of the posterior fangs in this species). However, my tooth counts are almost invariably greater than those given by Raxworthy and Nussbaum, and my tooth count for the paratype of *P. kely* and one specimen of *P. sokosoko* were 12+2, which are the lowest values I obtained (Table 2).

acter). State 0 is rare among Malagasy colubrids. Apart from *Pararhadinaea* and *Liophidium,* only *Dromicodryas* and *Micropisthodon* have this state, whereas all other genera have state 1. The state in the hypothetical ancestor is unknown (?). However, Savitzky (1981) postulated a derivation of *Liophidium* from snakes with greatly enlarged posterior fangs based on the feebly enlarged posterior teeth in *Liophidium*; this state was used as an alternative coding for the ancestor in the phylogenetic analyses.

7. A maxillary diastema may be absent (0) or present (1). *Pseudoxyrhopus* is scored as polymorphic (01) because of intraspecific variation. *Liophidium* and *Pararhadinaea* lack a maxillary diastema (state 0), whereas *Exallodontophis* has a diastema (state 1). In *Heteroliodon* a small gap was present in one specimen (no gap in another specimen), but I scored it as 0 because the gap is less than the width of a tooth. The ancestral condition is unknown (?), although a diastema is more commonly present in Malagasy colubrids.

8. A pale labial stripe continuous from the rostral scale to the nape collar is absent (0) or present (1). *Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon* are coded 1, whereas *Pararhadinaea* and *Liophidium* are coded 0. A labial stripe complete from the rostral scale to the nape collar is an unusual pattern, and the ancestor is scored 0.

In *Heteroliodon, Exallodontophis,* and all species of *Pseudoxyrhopus* a white stripe begins on the rostral scale, traverses the upper labials, and is continuous with a light nape collar except in those species of *Pseudoxyrhopus* lacking a collar (Fig. 17; see also Figs. 1, 2, 11, 14; and figures and descriptions by Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). In virtually all individuals (*Heteroliodon* and some individual *Pseudoxyrhopus* are exceptions) a peculiar short spur extends dorsally across the lateral edges of each internasal scale from the rostral portion of the stripe (Figs. 2, 17). The stripe is sometimes interrupted

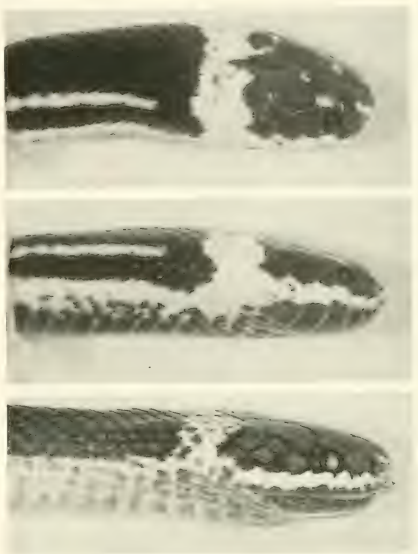

Figure 17. Labial and head patterns in the *Pseudoxyrhopus* group (see character 8). Approximately ×2.27. Top to bottom: Dorsal view of the head of *Exallodontophis albignaci* (UMMZ 203642), lateral view of the head of *E. albignaci* (UMMZ 203642), and lateral view of the head of *Pseudoxyrhopus oblectator* (MCZ 182292; holotype). The unusual pale spurs across the lateral edges of the internasals are visible in both specimens (less distinct in the *P. oblectator* due to camera angle).

below the eye and, rarely, by a dark spot on the rostral scale. The stripe is vivid (not obscured by a wash of dark pigment, as occurs commonly in colubrids) and usually is bordered above and below by black pigment (in *Heteroliodon* the labial border is white and thus the ventral border of the labial stripe is not defined).

Some variation is found within *Pseudoxyrhopus.* The internasal spurs are lacking in the only known specimen of *P. ankafinaensis* and occasional specimens of *P. tritaeniatus,* whereas in some specimens of *P. microps* and *P. tritaeniatus* the spurs broaden and completely surround the nostrils. In juveniles of *Pseudoxyrhopus microps* and in an adult with a very indistinct collar (CM 119068) the labial stripe and

collar are continuous (Raxworthy and Nussbaum, 1994, fig. 14). *Pseudoxyrhopus heterurus, P. imerinae, P. quinquelineatus,* and *P. sokosoko* lack collars in known specimens, but the labial stripe otherwise has the same disposition as in the collared species (juveniles of *P. heterurus* are unknown, but juveniles of the other three lack distinct collars; Fig. 13). In *P. quinquelineatus* the entire anterior portion of the snout is involved in the extensions of the labial stripe, and this may be true in *P. imerinae* (the only specimen examined was very faded).

In *Pararhadinaea* an irregular light labial stripe may be present or the supralabials may be irregularly spotted. However, when a stripe is present it is less discrete than in the other three genera and is obscured by a dense suffusion of dark pigment; it is separated from a nape collar by a broad dark postocular stripe that is continuous with dorsolateral stripes on the body (Fig. 18). Species of *Liophidium* often have light labial stripes, but these generally do not continue across the rostral scale and often end well short of it. Nape collars are present only in some species of *Liophidium* (e.g., in *L. therezieni* and some individuals of *L. rhodogaster*); when present they are usually at least partially separated from the labial stripe by a narrow dark band or row of spots.

9. Midbody scale rows are 17 (0) or 19 or more (1). *Pararhadinaea, Heteroliodon,* and *Exallodontophis* have 17 scale rows (0), whereas *Pseudoxyrhopus* has 19–25 (1). All Malagasy species of *Liophidium* have 17 midbody scale rows, although *L. mayottensis* from the Comoro Islands has 19; separate analyses were conducted coding *Liophidium* as 0 or as polymorphic (01). The ancestral condition is uncertain (?).

10. The number of dorsal scale rows may be the same posteriorly as at midbody (0) or dorsal scales may undergo posterior reduction (1). Dorsal scales are not reduced in *Exallodontophis, Heteroliodon,* or *Pararhadinaea* (0), whereas they undergo posterior reduction involving scale rows 4 and/or 5 in all species of *Pseudoxyrhopus* (1). Some species of *Liophidium* undergo posterior reduction involving rows 4 or 5, whereas other species are unreduced; thus, *Liophidium* is scored as polymorphic (01). The ancestral condition is unknown (?).

11. Activity patterns are either diurnal (0) or nocturnal (1). All observations indicate that species of *Liophidium* are diurnal (0), whereas *Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon* are nocturnal (1). A single observation for *Pararhadinaea melanogaster* suggests that it may be diurnal (0), although in separate analyses it was also scored as uncertain (?). Because the ancestral condition is unknown, the ancestor was also scored as uncertain (?).

Raxworthy and Nussbaum (1994) stated that *Pararhadinaea melanogaster* was probably nocturnal, but definitive observations are available only for MNHN 1982-1220; these data indicate that *P. melanogaster* is probably diurnal. Charles P. Blanc (in litt., 11 February 1999), who collected MNHN 1982-1220, provided the following observations paraphrased from his field notes:

> —The snake was collected on the coast 19 December 1972, in native forest on the ground. . . . I found this snake in the morning. As far as I can remember it was in the middle of the morning and the snake was active, perhaps disturbed by myself or by the trees [being cleared]. The snake was collected among logs and wood cut material, in a splendid lowland evergreen rainforest just being cut down, near the front of clearing on a sandy beach intended to become an industrial coconut plantation.

Thus, although these data do not rule out the possibility of the snake being disturbed from seclusion, taken at face value they indicate diurnality for *Pararhadinaea melanogaster.*

The three observations for *Heteroliodon* include being caught in a pitfall trap (time of day not reported), within a granite crevice, and within a rotten log, all during the day (Raxworthy and Nussbaum, 1994: 27–

Figure 18. Lateral view of the head and anterior body of *Pararhadinaea melanogaster* (MNHN 1982-1220, holotype of *P. m. marojejyensis*). Note the lack of a discrete light labial stripe and the dark bar separating the light colors of the upper labials and nape. Compare with Figure 17. Approximately ×4.8.

28). I interpret these to indicate nocturnality for this species, as did Raxworthy and Nussbaum (1994: 33). *Exallodontophis albignaci* was collected dead on a road in the morning, probably killed the previous night (Domergue, 1984); it was also caught in pitfall traps (time of day not reported) and within the soil under a large log during the day (Raxworthy and Nussbaum, 1994). As with *Heteroliodon*, I interpret these observations to indicate nocturnality.

12. Adult SVL is less than 650 mm (0) or greater than 800 mm (1). All species of *Liophidium, Pararhadinaea, Heteroliodon,* and *Exallodontophis* have state 0 (greatest SVLs 600 mm, 202 mm, 268 mm, 370 mm, respectively). Most species of *Pseudoxyrhopus* are <650 mm adult SVL (state 0), whereas *P. microps, P. tritaeniatus,* and *P. ankafinaensis* attain sizes >800 mm adult SVL (state 1). *Pseudoxyrhopus* is thus scored as polymorphic (01). The ancestral state is uncertain (?).

13. The morphology of individual teeth is unmodified (0) or modified (1). The teeth of *Pseudoxyrhopus* are curved, sharply pointed, and continuously tapering toward the tips (Fig. 6), which is the usual condition in colubrids and other caenophidians (state 0). These characters vary slightly among the species of *Pseudoxyrhopus*. For example, the teeth in *P. quinquelineatus* and *P. imerinae* are straighter, more robust, and less sharply pointed than those in the other species. The dentary teeth in *Pseudoxyrhopus* are usually straighter than the maxillary teeth (Fig. 6). However, the teeth of *Heteroliodon, Pararhadinaea,* and *Liophidium* are short, relatively straight, and have blunt tips that are slightly compressed anteroposteriorly. The distal portion of each tooth is slightly flared compared with the middle; thus, the teeth do not taper continuously toward the tips. This is considered a modified condition (state 1). Savitzky (1981, fig. 1i) illustrated the morphology for *Liophidium,* which is basically similar to that of *Heteroliodon* and *Pararhadinaea*.[14] However, the teeth of *Exallodontophis* are in some respects intermediate between the extremes represented by *Liophidium* and *Pseudoxyrhopus*. The anterior maxillary teeth of *Exallodontophis* are short, relatively straight, and rather blunt, but their tips are not expanded or compressed to the degree in *Liophidium*. In contrast, the anterior dentary teeth of *Exallodontophis* are straight, stout, rather bluntly pointed, and slightly compressed. The condition in *Exallodontophis* is thus somewhat ambiguous but is more similar to the condition in *Pseudoxyrhopus* and is scored 0. The ancestral condition is assumed to be 0 because the modified tooth morphology is unknown in other Malagasy snakes and is rare in colubrids generally.

14. The anterior dentary teeth are subequal to or larger than the posterior dentary teeth (0), or the posterior dentary teeth are larger and more robust than the anterior teeth (1). *Pseudoxyrhopus, Exallodontophis,* and *Heteroliodon* have state 0 (Figs. 6, 10, 12). *Pararhadinaea melanogaster* has state 1 (Fig. 7). *Liophidium* is

[14] Tooth form varies somewhat among species of *Liophidium,* and the morphology in *L. rhodogaster* illustrated by Savitzky (1981) is the extreme. In other species the teeth are blunt and compressed at the tips, but the degree of distal expansion varies. For example, in both *L. torquatum* and *L. vaillanti* the anterior maxillary teeth are more expanded distally than the posterior teeth (personal observations).

scored as 0 for this character even though no distinction is made between anterior and posterior dentary teeth; all dentary teeth are subequal. The ancestral condition is assumed to be 0. Raxworthy and Nussbaum (1994, table 7) stated that the anterior dentary teeth were larger than the posterior ones in *Pseudoxyrhopus* but not in *Heteroliodon* or *Pararhadinaea*. Their scoring for *Pararhadinaea* was based on *Exallodontophis albignaci*, and my observations for both *Heteroliodon* (Fig. 12) and *Exallodontophis* are that the anterior and posterior dentary teeth are approximately the same size (state 0).

15. The number of posterior dentary teeth is less than 10 (0) or more than 12 (1). Exallodontophis, Heteroliodon, and *Pararhadinaea* have state 0, whereas *Pseudoxyrhopus* is polymorphic (01) (see footnote 3, Table 2). I coded *Liophidium* as state 1 because of the large number of dentary teeth in general, even though there is no distinction between the anterior and posterior dentary teeth. The ancestral state is uncertain (?).

16. The number of ventral scales is less than 200 (0) or more than 200 (1). Exallodontophis, Heteroliodon, and *Pararhadinaea* have state 0, whereas both *Pseudoxyrhopus* and *Liophidium* are interspecifically variable and are coded as polymorphic (01). The ancestral state is uncertain (?).

PHYLOGENY OF THE *PSEUDOXYRHOPUS* GROUP

Parsimony analysis of the data matrix (Table 5) using the standard character codings resulted in three equally most parsimonious trees (MPTs) of 21 steps (Fig. 19). Trees 1 and 2 (Fig. 19) are fully resolved, whereas tree 3 has an unresolved basal polytomy. The three trees differ in the placement of *Pararhadinaea*, and the strict concensus of all three MPTs is identical to tree 3. The MPTs had a CI (excluding uninformative characters) of 0.68 and an RI of 0.89. Phylogenetic trees using the alternative polymorphism codings for characters 1, 4, and 9 (Table 5) yielded four MPTs of 24 steps (CI excluding uninformative characters = 0.67; RI = 0.87). Three of these trees had topologies identical to the MPTs using the standard codings; the fourth was identical to tree 2 (Fig. 19) except that it contained a polytomy for *Pseudoxyrhopus–Exallodontophis–Heteroliodon*.

Either of two alternative character codings force resolution of the MPT for the data as either tree 1 or tree 2 (Fig. 19). These alternatives are, respectively, for character 3 (*Pararhadinaea* = state 1) and character 6 (ancestor = state 1), resulting in single MPTs of 21 steps in each case when no alternative polymorphic character codings are used. In the first case, the alternative coding results in another synapomorphy shared by *Pararhadinaea* and *Pseudoxyrhopus–Exallodontophis–Heteroliodon* (*P-E-H*) (tree 1). In the second case, coding the ancestral condition of the maxillary fangs the same state as that shared by *P-E-H* results in recognition of the state 0 shared by *Pararhadinaea* and *Liophidium* as a synapomorphy (tree 2). Thus, the phylogenetic position of *Pararhadinaea* is ambiguous, and it seems preferable to consider the strict consensus topology (Fig. 19, tree 3) as the best current estimate of phylogeny for the *Pseudoxyrhopus* group.

In any case, the hypothesis of monophyly for *Pseudoxyrhopus–Heteroliodon–Pararhadinaea* to the exclusion of other Malagasy colubrids (Raxworthy and Nussbaum, 1994), including *Liophidium*, is not strongly supported when characters shared with *Liophidium* are considered. If *Liophidium* is excluded from the analysis, a single MPT is obtained. It has 17 steps and a topology identical to the trees in Figure 19 with *Liophidium* pruned from them.

The ambiguous relationship of *Pararhadinaea* to the other genera under consideration emphasizes how few characters support a clade containing *Pseudoxyrhopus, Exallodontophis, Heteroliodon,* and *Pararhadinaea* to the exclusion of *Liophi-*

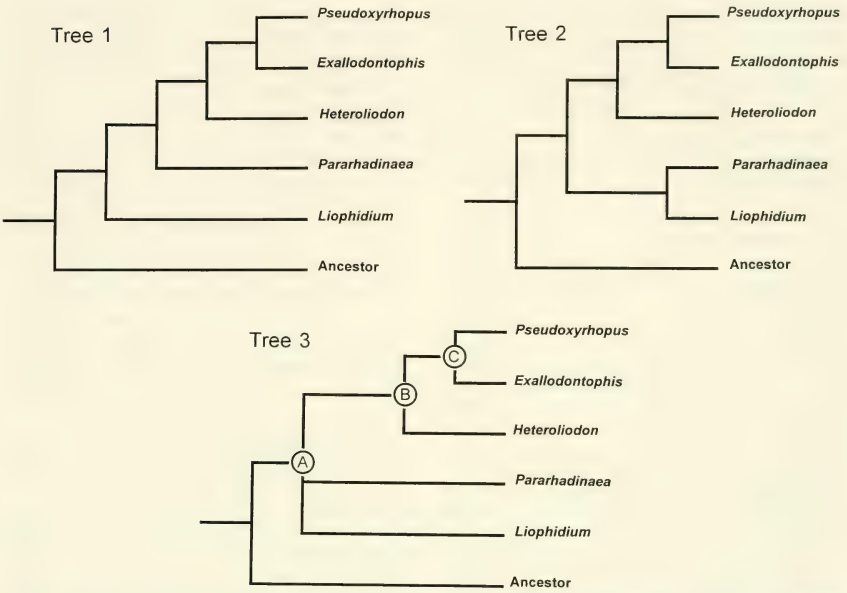

Figure 19. Three equally parsimonious trees reconstructed from the standard codings of character data in Table 5. Tree length = 21 steps, CI (excluding uninformative characters) = 0.68, RI = 0.89. The strict consensus of all three trees is identical to tree 3. Nodes A–C in tree 3 are referred to in the text and in Table 6.

dium. Although only characters 1 and 2 (Table 5) unambiguously support the inclusion of *Liophidium* in the *Pseudoxyrhopus* group, support for inclusion of *Pararhadinaea* in the group is equally weak. Only character 5 is an apomorphy supporting the relationship of *Pararhadinaea* to *P-E-H* in tree 1 (Fig. 19) under either ACCTRAN or DELTRAN character optimization. However, for tree 2 (Fig. 19) only character 13 under DELTRAN optimization supports the clade *Pararhadinaea–Liophidium*. Further resolution of the relationships of *Pararhadinaea* will not be possible without the addition of other characters or elimination of uncertain (?) codings for ancestral character states (accomplished objectively by more definitive resolution of outgroups). Eliminating the uncertain codings for some characters in Table 5 would make either of the fully resolved topologies (Fig. 19, trees 1 and 2) more favorable under parsimony (e.g., characters 5, 6, 7, 11).

None of the MPTs (Fig. 19) places *Exallodontophis albignaci* and *Pararhadinaea melanogaster* as sister taxa, as would be implied by the union of both species in *Pararhadinaea* according to the previous taxonomy. In fact, the shortest trees constraining monophyly of these two taxa are 6 steps longer than the MPTs using the standard character scorings (five trees of 27 steps; CI excluding uninformative characters = 0.54; RI = 0.22). This analysis provides strong support for removal of *albignaci* from *Pararhadinaea*.

Table 6 shows apomorphies under ACCTRAN optimization for clades in the strict consensus phylogeny (Fig. 19, tree 3,

TABLE 6. APOMORPHIES FOR THE STRICT CONSENSUS OF RELATIONSHIPS AMONG GENERA OF THE *PSEUDOXYRHOPUS* GROUP (SEE FIG. 19, TREE 3, FOR LABELED NODES). STANDARD CHARACTER CODINGS (TABLE 5) WERE OPTIMIZED USING ACCTRAN UNDER MAXIMUM PARSIMONY.

Branch	Character no.[1]	Change
Ancestor ↔ node A[2]	1	0 ⇔ 1
	2	0 ⇔ 1
	13	0 ⇔ 1
Node A → node B	3	0 ⇒ 1
	6	0 ⇒ 1
	8	0 ⇒ 1
	11	0 ⇒ 1
Node B → node C	4	0 ⇒ 1
	7	0 → 1[3]
	13	1 ⇒ 0
Node C → *Pseudoxyrhopus*	9	0 ⇒ 1
	10	1 ⇒ 0
Node A → *Pararhadinaea*	14	0 ⇒ 1
Node A → *Liophidium*	5	1 ⇒ 0
	15	0 ⇒ 1

[1]Characters 12 and 16 change within terminal taxa (*Pseudoxyrhopus* and/or *Liophidium*) and thus do not appear in the table.

[2]Direction of change between ancestor and node A is not determinable.

[3]This change is not the only most parsimonious reconstruction possible, but all others are unambiguous changes.

standard character codings). The clade *P-E-H* is the most strongly supported, with four unambiguous character transformations supporting it. Each of these transformations is unique and unreversed using the present character codings, but resolution of the uncertain (?) codings for the ancestor could change that assessment. Unambiguous synapomorphies of the clade *P-E-H* are enlarged median dentary teeth, greatly enlarged maxillary fangs, and the distinctive head pattern. *Pseudoxyrhopus* and *Exallodontophis* are united by one unique and unreversed synapomorphy (the presence of a diastema in the dentary tooth row, character 4) and a reversal (tooth form, character 13). Change in character 7 (maxillary diastema) along the branch between nodes C and D (Table 6) occurs only because ACCTRAN was used and *Pseudoxyrhopus* is polymorphic for this character. Character 13 is the only character for which a disparity between the minimum possible changes (1) and the estimated tree changes (2) exists.

Another character potentially corroborating the clade *Pseudoxyrhopus–Exallodontophis* relative to *Heteroliodon* is the presence of pale spurs across the lateral portions of the internasals from the rostral scale (see discussion of character 8). I did not code this unusual feature separately, considering it part of the labial stripe complex. However, despite some variation within *Pseudoxyrhopus,* this character would map to the branch between nodes B and C (Fig. 19, tree 3) and offers additional support for the sister relationship of *Pseudoxyrhopus* and *Exallodontophis.*

CHARACTER EVOLUTION AND RELATIONSHIPS WITHIN THE *PSEUDOXYRHOPUS* GROUP

The phylogenetic hypotheses in Figure 19 bear on previous discussions of character evolution and relationships within *Pseudoxyrhopus.* Regardless of the coding of the hypothetical ancestor, reconstructed plesiomorphic conditions for the *Pseudoxyrhopus* group (basal ingroup node in Fig. 19) and for *Pseudoxyrhopus* itself include small body size (character 12), fewer than 11 posterior dentary teeth (character 15), and fewer than 200 ventral scales (character 16). The contrasting derived conditions of the *Pseudoxyrhopus microps* group (including *P. microps, P. tritaeniatus,* and *P. ankafinaensis*) confirm the hypothesis that the *P. microps* group is monophyletic within *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994); these species are also unique among *Pseudoxyrhopus* species in having 25 midbody dorsal scale rows, which is probably a derived character because of its rarity among Malagasy colubrids. (Alternative interpretations of other character variation within *Pseudoxyrhopus* result in some other hypotheses of relationships than those given by Raxworthy and Nussbaum, 1994.)

More interesting from the standpoint of natural history are implications of the phy-

logenetic hypotheses in Figure 19 for the evolution of dentitional characters. Setting aside the hinged teeth and modified tooth replacement characteristic of all these snakes, only species of *Pseudoxyrhopus* lack unusual characteristics of dental configuration or of the morphology of individual teeth; their dental characters do not immediately suggest features not observed elsewhere among many colubrids (Fig. 6). This is not the case for the other genera. *Exallodontophis* is characterized by the highly unusual form of the maxilla, an exceptionally broad maxillary diastema, and unusually large median maxillary teeth (Fig. 10). *Pseudoxyrhopus,* the sister group of *Exallodontophis,* and *Heteroliodon,* the immediate outgroup of *Pseudoxyrhopus–Exallodontophis,* share a similar configuration of the maxillary dentition (Figs. 6, 12). Thus, the unusual dentitional characteristics of *Exallodontophis* probably evolved from a condition in which the number of maxillary teeth was already somewhat reduced (character 5), but the other unusual characters evolved within the *Exallodontophis* lineage.

The peculiar form of the teeth in *Heteroliodon, Pararhadinaea,* and *Liophidium* (character 13) has a more complex evolutionary history under any of the hypotheses in Figure 19. Tree 1 requires that the derived tooth morphology either evolved twice (once in *Heteroliodon* and once in *Pararhadinaea–Liophidium*) or was a plesiomorphic state for the *Pseudoxyrhopus* group that was subsequently lost in the lineage leading to *Pseudoxyrhopus* and *Exallodontophis.* Either of the hypotheses illustrated in trees 2 and 3 (Fig. 19) requires a basal origin and subsequent reversal of the unusual tooth morphology shared by these genera. However, a less parsimonious hypothesis is that the unusual tooth morphology is nonhomologous in these genera, i.e., it has evolved multiple times within this group. Thus, not only does this small group of Malagasy colubrids show exceptional diversity in tooth characters and the overall configuration of the dentition, but the phylogenetic hypotheses suggest a complex evolutionary history (multiple origins or reversals) for some individual characters (tooth form, maxillary diastema) but not others (enlarged dentary teeth and maxillary fangs). Precisely how the evolution of these characters is correlated with prey acquisition behaviors remains to be determined.

MONOPHYLY OF TERMINAL TAXA

One implicit assumption in this (and indeed all) phylogenetic analyses is the monophyly of the terminal taxa. This assumption is not problematic for *Exallodontophis, Heteroliodon,* and *Pararhadinaea*; the derived dentitional morphologies for these monotypic genera have already been documented. The assumption is more problematic for *Pseudoxyrhopus* and *Liophidium.* The combination of characters given for the diagnosis of *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994) includes mostly rather common colubrid characters (enlarged, ungrooved rear fangs), although the presence of 19 or more midbody scale rows and posterior scale reduction (introduced herein) distinguish it from *Exallodontophis, Heteroliodon,* and *Pararhadinaea.* However, *Pseudoxyrhopus* is characterized mainly by lacking the autapomorphies of the other genera. Other character systems need to be investigated to properly diagnose *Pseudoxyrhopus.*

Two of the most widely cited characters diagnosing *Liophidium* (seven described and several undescribed species) are hinged teeth and modified tooth replacement. These characters are now seen as synapomorphies for a larger clade of Malagasy snakes (Table 6). There seems to be much variation in size, body proportions (e.g., relative tail lengths), scale characters, tooth morphology (Savitzky, 1981), and hemipenial morphology (Cadle, 1996a: 382) within *Liophidium.* Earlier in this century (e.g., Mocquard, 1909), the species of *Liophidium* were partitioned among *Liophidium, Polyodontophis,* and *Idiophis,* distinguished primarily on the

basis of characters of the maxillary and dentary dentition. Guibé (1958) placed the Malagasy species of all these genera in *Liophidium* and stated that the rationale was to be given in a separate publication to be coauthored with A. R. Hoge. That report was never published, but early diagnoses for these genera (e.g., Boulenger, 1893, 1896; Mocquard, 1901) show little distinction. For example, the only character that differs in Boulenger's diagnoses of *Liophidium* and *Polyodontophis* is whether the posterior teeth are "feebly enlarged" or not, which is rather variable and subjective.

Other characters sometimes cited as synapomorphies for *Liophidium* (anterior displacement of the dentary–compound bone articulation in the lower jaw, free posterior dentigerous process on the dentary, highly developed intramandibular kinesis, long lateral process of premaxillae overlapping anterior ends of maxillae) have been verified in few species because of their rarity in collections. Virtually all comparative studies have been based on the species *L. rhodogaster, L. torquatum,* and *L. vaillanti* and often only one or two of these (Morgan, 1973; Savitzky, 1981, 1983; Domergue, 1983; Cadle, 1996a: 381–382). Until these putative synapomorphies and other characters are surveyed for a broader array of species the monophyly of *Liophidium* will remain poorly corroborated. For example, it is quite possible that some of the "diagnostic" characters of *Liophidium* actually document the monophyly of a smaller set of species, just as the hinged teeth and tooth replacement pattern corroborate the monophyly of a larger set. Thus, the character interpretations presented here should be considered provisional, and additional comparative study of species of *Liophidium* should be undertaken. One character of potential significance in diagnosing *Liophidium* is the asymmetry of the hemipenial lobes, which has been noted in several species (e.g., Domergue, 1983; Ziegler et al., 1996; see also footnote 11). This unusual character may prove diagnostic for *Liophidium,* but given that hemipenes of *Pararhadinaea* and *Exallodontophis* are as yet undescribed, asymmetry of lobes may also be more widespread within the *Pseudoxyrhopus* group.

ARE THE MALAGASY AND AFRICAN HINGED-TOOTH SNAKES CLOSELY RELATED?

The phylogeny and hypothesized character evolution in Figure 19 are based on few, albeit highly unusual, characters shared by *Liophidium* and *Pseudoxyrhopus–Exallodontophis–Heteroliodon–Pararhadinaea* (*P-E-H-P*). Nonetheless, I question the significance of morphological and behavioral differences between *P-E-H-P* and other Malagasy colubrids, specifically *Liophidium,* as emphasized by Raxworthy and Nussbaum (1994). Thus, I am dubious that the closest relatives of *P-E-H-P* or the *Pseudoxyrhopus* group should be sought outside Madagascar. Despite these reservations, additional comparisons between the *Pseudoxyrhopus* group and the African genera said to be related to *Lycophidion* and *Mehelya* are probably warranted because many of their dentitional characters are similar, although in various combinations in the different genera (personal observations; see also Parker, 1933). These African genera, Group II of Bogert (1940), are *Hormonotus, Gonionotophis, Mehelya, Lycophidion,* and *Chamaelycus.*

Both the maxillary and dentary dentitions of Bogert's (1940) Group II genera are similar in many unusual characters to those of some members of the *Pseudoxyrhopus* group. Like the *Pseudoxyrhopus* group, hinged teeth are found in *Lycophidion, Mehelya,* and *Chamaelycus.* At least some species of *Lycophidion, Mehelya, Chamaelycus,* and *Hormonotus* have a broad diastema in the middle of the maxilla, which is preceded by relatively enlarged robust teeth (Parker, 1933). However, neither the diastema nor the teeth preceding it are developed to the same degree as in *Exallodontophis. Lycophidion,*

Mehelya, Chamaelycus, and *Hormonotus* also have an anterior series of dentary teeth that increase in size to about the fifth or sixth tooth, followed by a series of smaller teeth (Bogert, 1940; Parker, 1933; personal observations). In *Chamaelycus, Hormonotus,* and some species of *Lycophidion* a median pair of dentary teeth is exceptionally enlarged and is followed by a diastema, as in *Pseudoxyrhopus* and *Exallodontophis.* Despite these shared unusual characters, none of which appear in precisely the same combinations as in the *Pseudoxyrhopus* group, the morphology of the dentition and dentigerous bones in Bogert's Group II genera is otherwise dissimilar to that in any Malagasy colubrids. For example, the African genera lack enlarged posterior fangs. Some similar dentitional characters (median maxillary diastema and enlarged anterior dentary teeth) are also found in other African snakes, such as some members of Bogert's (1940) Group I (e.g., *Lamprophis olivaceus*; Boulenger, 1893, fig. 22). These characters led Boulenger (1890) to hypothesize that *Pseudoxyrhopus* was related to these "lycodonts," a large, nebulous assemblage, but he was not more specific.

An additional complication in evaluating possible relationships between the *Pseudoxyrhopus* group and Bogert's (1940) Group II is that the monophyly of Group II has not been extensively documented. Bogert explicitly deemphasized hemipenial characters in his classification except the divided or undivided nature of the sulcus spermaticus. His groups represented a subjective impression of genera "believed to represent the most closely allied forms" (Bogert, 1940: 10). McDowell (1987), without extensive commentary, implicitly set apart *Mehelya* and *Gonionotophis* from a cluster of genera including *Lycophidion, Chamaelycus, Hormonotus,* and *Bothrolycus,* the last of which Bogert (1940) had included in his Group I. In the only biochemical study of this group, Cadle (1994) found no support for a strong association of either *Lycophidion* or *Gonionotophis* specifically with *Mehelya,* the only member of Group II represented by a reference antiserum, when their albumins were compared by microcomplement fixation (no samples of the other Group II genera were available). Too much should not be made of these unidirectional immunological comparisons, although reciprocity and rate-tested data were considered reliable in that study. Also, in Cadle's (1994) study, Bogert's Groups I and II formed a well supported clade. Thus, although Cadle (1994) found no support for a phyletic association between *Lycophidion* or *Gonionotophis* and *Mehelya,* all of these genera were part of a larger well-supported clade. This result suggests that relationships among these genera might be more complex than suggested by Bogert's groupings. In particular, the morphology of the hemipenis and dentition of *Gonionotophis* is unlike that of the other genera of Group II, but we currently lack a comprehensive understanding of the phylogenetic significance of these characters in African colubrids.

Bogert (1940) had examined hemipenes of all Group II genera except *Gonionotophis,* whose hemipenis seems not to have been described in detail. Hemipenes of all Group II genera except *Gonionotophis* are deeply divided (bilobed) and entirely spinose and have centrifugal sulci spermatici. However, the hemipenis of *Gonionotophis granti* is nonbilobed or very shallowly bilobed and has an unusual nude apical structure with a shallow delimiting groove on the asulcate side and a divided sulcus spermaticus with centrifugal branches (personal observations based on the fully everted organs of MVZ 176439). McDowell (1987: 37) independently noted the "hardly bilobate" structure of the hemipenis in *G. granti.* Except for the centrifugal branches of the sulcus spermaticus, these features are unlike those of any other members of Group II. Furthermore, at least two species of *Mehelya, M. crossi* and *M. guirali,* have a large basal nude pocket, which has not been reported in other gen-

era of Group II (personal observations on the inverted organs of MVZ 75748 and MVZ 81462, respectively). The nonbilobed organ and unusual apical structure of *Gonionotophis* are probably derived features (see Myers, 1973; Cadle, 1996b). Thus, the closest relatives of *Gonionotophis* might be sought among other African colubrids with nonbilobed hemipenes rather than among Group II genera, although one cannot exclude the possibility that these characters are simply autapomorphies of *Gonionotophis* within Group II. Nonetheless, *Gonionotophis* differs in other significant ways from the Group II genera.

Notably, all genera of Group II except *Gonionotophis* have a diastema in the middle of the maxillary tooth row and have enlarged median dentary teeth and a dentary diastema. Loveridge (1939) seems to have been the first to specifically suggest a relationship between *Gonionotophis* and *Mehelya,* but his inference was based solely on the confused synonymy of species in the two genera in the 19th century literature: "From this [i.e., the confused species and generic synonymies] it will be concluded that the relationship between the two genera . . . is of the closest nature" (Loveridge, 1939: 131). Loveridge presented no morphological data to bolster this conclusion. *Gonionotophis* and *Mehelya* do share unusual lateral expansions on the vertebrae, although these are not as extensively developed in *G. granti* as in *M. capensis* and *M. crossi* (personal observations); *Gonionotophis* also lacks the prezygopophyseal expansions observed in *Mehelya* (personal observations; see Bogert, 1964). However, none of these unusual vertebral characters are known in the other Group II genera. The immunological data and the differences in dentition and hemipenial morphology between *Gonionotophis* and *Mehelya* suggest that a relationship between these two genera may be more remote than current wisdom suggests. The only dietary records for *Gonionotophis* are two frogs (Shine et al., 1996). This record contrasts with the primarily reptilian (especially lizard) diets characteristic of the other Group II genera (Parker, 1933; Branch, 1976; Savitzky, 1981; Broadley, 1983; Shine et al., 1996), although *Mehelya* is known to occasionally consume frogs, especially bufonids (Shine et al., 1996).

Hemipenial morphology of *Lycophidion, Mehelya,* and and other Group II genera except *Gonionotophis* are similar to those of *Pseudoxyrhopus* and *Liophidium* only in superficial ways that do not suggest special relationship. The known hemipenes of *Lycophidion* and *Mehelya* are deeply bilobed and entirely spinose (for descriptions and illustrations, see Bogert, 1940; Doucet, 1963; Branch, 1976; personal observations). Hemipenes of *Lycophidion* and *Mehelya* differ from those of any known Malagasy colubrids in having centrifugal sulci spermatici, which divide more basally in most species of *Lycophidion* and *Mehelya* than in *Pseudoxyrhopus* and *Heteroliodon* (Doucet, 1963; Broadley, 1983; personal observations of *M. crossi* and *M. guirali* based on MVZ 75748 and 81462, respectively). The sulcus spermaticus is centrolineal in *Pseudoxyrhopus, Heteroliodon,* and *Liophidium,* but the orientation is unknown in *Exallodontophis* and *Pararhadinaea.* Some species of the African genera have unusual structures, such as the trilobed apical morphology of *Lycophidion variegatum* (Branch, 1976) and large nude basal pockets in *Mehelya* (personal observations). Hemipenes of *Mehelya* have extremely long, narrow lobes unlike *Pseudoxyrhopus* (Bogert, 1940; Doucet, 1963; personal observations) but reminiscent of some species of *Liophidium* (Domergue, 1983). No clearly derived hemipenial structures are known to be shared by *Lycophidion* or *Mehelya* and any Malagasy colubrids.

Until more comprehensive phylogenetic analyses including these genera have been completed it will not be possible to evaluate the extent to which the unusual dentition and jaw characters shared by these

African and Malagasy snakes are due to common ancestry, or are convergent specializations related to similar diets. The complexity of the colubrid radiation in Africa (Cadle, 1994) and the questionable monophyly of the clade of African hinge-toothed snakes (Bogert's Group II) makes these analyses exceedingly complex.

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SPECIMENS OF THE *PSEUDOXYRHOPUS* GROUP EXAMINED

Museum abbreviations are as follows.

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum, London
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley

MNHN	Muséum National d'Histoire Naturelle, Paris
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt
SMNS	Staatliches Museum für Naturkunde in Stuttgart
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Washington, D.C.

Unless otherwise noted, localities for these specimens were given by Raxworthy and Nussbaum (1994) for *Exallodontophis, Heteroliodon,* and *Pseudoxyrhopus* and by Domergue (1983) for *Liophidium.* Observations on dentition were made on specimens denoted as follows: SK = dry skull (all teeth examined); MT = maxillary teeth examined; DT = dentary teeth examined.

Exallodontophis albignaci. MNHN 1982.1221 (MT)(holotype). UMMZ 203642 (MT) (Antsiranana Prov.: Sambava Fivondronana: Marojejy Reserve, Manantenina River, 350 m elevation).

Heteroliodon occipitalis. BMNH 1946. 1.12.28 (MT) (holotype), 1930.7.1.238 (MT).

Liophidium apperti. MNHN 1982.442 (MT) (holotype).

Liophidium chabaudi. MNHN 1978. 2789 (MT) (holotype), 1978.2788 (MT).

Liophidium rhodogaster. MCZ 180381 (MT), 180382 (MT), 181169 (MT), 181170 (MT), 181171 (SK), 181172 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Talatakely, Ranomafana National Park, approximately 950–1,000 m elevation).

Liophidium therezieni. MNHN 1982. 444 (MT) (holotype), 1978.1425 (MT).

Liophidium torquatum. BMNH 1946. 1.1.38 (MT) ("Madagascar," holotype), 89. 4.11.10 ([Toamasina Prov.]: Antongil Bay). MCZ 181303 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: 6 km (by Route 25) W. Andranomaitso between Ifanadiana and Kianjavato, approximately 500–600 m elevation). MCZ 181305 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Ranomafana town, approximately 600 m elevation).

Liophidium trilineatum. BMNH 1946. 1.15.66 (MT) (holotype) ([Toliara Prov.]: Southwestern Madagascar).

Liophidium vaillanti. MNHN 1901.186, 1901.187 (MT) (syntypes) ([Toliara Prov.]: Fort Dauphin and Isaka). MCZ 22203 (SK) (locality unknown).

Pararhadinaea melanogaster. SMF 17885 (old number 7313.1a) (MT, DT) (holotype [Antsiranana Prov.: Fivondronana Nosy Be]: Insel Nossibé). SMNS 4235 (MT, DT) (holotype of *Rhabdotophis subcaudalis* Werner, 1909. "Madagascar").

Pararhadinaea melanogaster marojejyensis. MNHN 1982.1220 (MT) (holotype [Antsiranana Prov.: Fivondronana Andapa]: "Forêt du massif montagneux du Marojejy" [Domergue, 1984]), here interpreted to be imprecise based on information provided by Charles P. Blanc. According to Blanc, the specimen was collected 19 December 1972 in pristine lowland rainforest on the coast.

Pseudoxyrhopus ambreensis. UMMZ 200061 (MT, DT), 200062 (MT), 200063 (MT), 203643, 203644.

Pseudoxyrhopus imerinae. BMNH 95.10.29.60 (MT, DT).

Pseudoxyrhopus kely. UMMZ 192022 (MT, DT).

Pseudoxyrhopus microps. CM 119068 (MT, DT).

Pseudoxyrhopus quinquelineatus. BMNH 93.9.6.2 (SK), 1930.7.1.236 (MT), 1930.7. 1.237 (MT, DT). USNM 149903 (MT, DT) ([Toamasina Prov.]: Perinet). MCZ 11651 (SK) ([Toamasina Prov.]: Swamp near Didy).

Pseudoxyrhopus sokosoko. UMMZ 203660, 203661 (MT), 209689 (MT).

Pseudoxyrhopus tritaeniatus. AMNH 60712 (MT, DT) (specific locality unknown). MNHN 1891.24 (MT) (holotype [probably Fianarantsoa Prov.]: "Betsileo"), 1898.7 (MT) (specific locality unknown). MCZ 180300 (Fianarantsoa Prov.: Fivondronana Ifanadiana: Route 25 between Ambatolahy and Ranomafana town),

182468 (SK) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Ranomafana National Park, mountain ridge N of Miaranony approximately 9.8 km [airline] WNW Tsaratanana, Faravory River, approximately 1,100 m elevation), 182480 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Talatakely, Ranomafana National Park, 970 m elevation).

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The Orbweavers of the Genera *Molinaranea* and *Nicolepeira*, a New Species of *Parawixia*, and Comments on Orb Weavers of Temperate South America (Araneae: Araneidae)

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THE ORBWEAVERS OF THE GENERA *MOLINARANEA* AND *NICOLEPEIRA,* A NEW SPECIES OF *PARAWIXIA,* AND COMMENTS ON ORB WEAVERS OF TEMPERATE SOUTH AMERICA (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. Two genera of araneid orb weavers are endemic in temperate South America: *Molinaranea* and *Nicolepeira. Molinaranea* has seven species, the new genus *Nicolepeira* has three. About 40 names are available for the 10 species. Two new species are included, along with 21 new synonyms. In addition, one new species of *Parawixia, P. chubut,* is described. The introduced European orb weaver *Zygiella x-notata* is common in temperate South America. Synapomorphies place *Molinaranea* close to *Parawixia* and *Eriophora.* The placement of *Nicolepeira* is uncertain.

INTRODUCTION

The lack of illustrations in older literature has heretofore prevented determination of common orb-weaving spiders from the temperate Neotropics. By using large museum collections, comparison of individuals from numerous separate expeditions has been possible.

The early describer was Nicolet (Levi, 1964). Nicolet was a French entomologist who lived part of his life in Chile; he died in 1872. His only publication is on the arachnids of Chile, in Gay's 1849 treatise on Chile (Nicolet, 1849). It contains descriptions of 297 species, most of them new (Bonnet, 1945: 35); for some species useful illustrations are presented.

Simon studied Chilean spiders (1884, 1887, 1888, 1896, 1901, 1904) and examined specimens of Nicolet that had been deposited in the Paris museum. Early in 1888, Simon reported that *Diphya* specimens of Nicolet were lost and that Nicolet's descriptions were not recognizable. In 1887, he referred to the poor condition of Nicolet's specimens. In 1896, Simon synonymized *Epeira flavipes* Nicolet with *Argiope trifasciata,* placed *Epeira gasteracanthoides* in *Glyptocranium* [=*Mastophora*], and synonymized *Epeira rectangula* with *E. labyrinthea* (the last in error, Piel, 2001). But Simon did not say whether he examined Nicolet's specimens. In 1896, Simon also described and named *Araneus phaethontis, A. surculorum,* and *A. titirus* as new species. In 1904, Simon synonymized *Epeira thalia, E. nigrata, E. inflata, E. erudita,* and *E. hispida* with *E. clymene.* Although Simon was aware of the unique pattern on the venter of the large *E. flaviventris,* he did not recognize that it was diagnostic, and that Nicolet had described the same species numerous times, usually on the basis of dorsal color variations of early instars, 2–5 mm in total length. Here I follow Simon's nomenclature, but instead of *flaviventris,* I use the older name *magellanica* for this common species. More recently, the name *cinaberina* has been used for this species by Mello-Leitão and by Schiapelli and Gerschman (1974). Specimens of *magellanica* were described earlier by Walckenaer (1847), who gave adequate characters and stated that the species came from the Strait of Magellan. Because only few other orb weavers occur there, no doubt exists as to its identity.

The few araneoid orb weavers found in Chile are listed in Table 1. Most are distinct from those of Peru to the north.

[1] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138-2902.

TABLE 1. CHILEAN ARANEID ORB WEAVERS OTHER THAN *MOLINARANEA* AND *NICOLEPEIRA*. (THE GENERA *EUSTALA*, *MANGORA*, AND *VERRUCOSA* HAVE NOT BEEN REVISED AND MAY HAVE SPECIES IN CHILE.).

	Distribution	Citation
Argiope trifasciata (Forskål, 1775)	Cosmopolitan	Levi, 1968
Araneus alhue Levi, 1991	Endemic in Chile	Levi, 1991
A. concepcion Levi, 1991	Endemic in Chile	Levi, 1991
A. huahun Levi, 1991	Endemic in Chile	Levi, 1991
A. talca Levi, 1991	Endemic in Chile	Levi, 1991
A. zapallar Levi, 1991	Endemic in Chile	Levi, 1991
Cyclosa serena Levi, 1999	Argentina	Levi, 1999
Larinia bivittata Keyserling, 1884	Southern South America	Harrod et al., 1991
Mastophora gasteracanthoides (Nicolet, 1849)	Endemic in Chile	Nicolet, 1849
Mecynogea erythromela (Holmberg, 1876)	Southern South America	Levi, 1997
Metepeira compsa (Chamberlin, 1916)	Northern Chile, Peru, Lesser Antilles, Brazil	Piel, 2001
M. galatheae (Thorell, 1891)	Argentina	Piel, 2001
M. rectangula (Nicolet, 1849)	Argentina	Piel, 2001
M. tarapaca (Piel, 2001)	Northern Chile, Southern Peru	Piel, 2001
Ocrepeira venustula (Keyserling, 1880)	Southern South America	Levi, 1993
Zygiella x-notata (Clerck, 1758)	Import from Europe	Levi, 1974

Some have spread from or into Argentina. The Argentine area of South America has some species from the tropics as well as extensions of species distributions over the Andes. Unfortunately, few collections are available from Patagonia, leaving our knowledge incomplete.

METHODS AND ACKNOWLEDGMENTS

The methods used here were described in Levi (1993). In the descriptions, the distances between the eyes of the anterior row are expressed as diameters of the anterior median eyes (in profile); distances between eyes of the posterior row are given as diameters of the posterior median eyes (in profile). The shape of the ocular quadrangle is measured outside the eyes. Features in illustrations are indicated by the face of a clock. All species included here are relatively large and easily examined. Males and females are easy to match as they are frequently collected together and have similar ventral markings on the abdomen.

The following collections were used:

AMNH American Museum of Natural History, New York, United States; N. Platnick, L. Sorkin

BMNH Natural History Museum, London, England; P. Hillyard, F. Wanless

CAS California Academy of Sciences, San Francisco, California, United States; W. J. Pulawski, D. Ubick, C. Griswold

FSCA Florida State Collection of Arthropods, Gainesville, Florida, United States; G. B. Edwards

IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; L. Baert

MACN Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; M. E. Galiano, C. L. Scioscia

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States

MLP Museo de Universidad Nacional, La Plata, Argentina; R. F. Arrozpide, C. Sutton, L. A. Pereira

MNHN Muséum National d'Histoire Naturelle, Paris, France; J. Heurtault, C. Rollard

MNRJ Museu Nacional, Rio de Janei-

ro, Brazil; A. Timotheo da Costa, A. B. Kury
NRMS Naturhistoriska Riksmuseet, Stockholm, Sweden; T. Kronestedt
PAN Polska Akademia Nauk, Warszawa, Poland; J. Prószynski, A. Slojewska, W. B. Jedryczkowski, T. Heflejt
ZMUC Zoologisk Museum, Copenhagen, Denmark; H. Enghoff, N. Scharff

I thank the curators of the collections for the time-consuming task of searching out and sending the specimens needed for study. C. Scioscia helped find some localities. W. Piel supplied me with some natural history observations. Laura Leibensperger aided in numerous ways. Lorna Levi, Laura Leibensperger, William Piel, and an anonymous reader read the draft of the manuscript and made valuable suggestions. R. Preston-Mafham provided me with black and white photographs. The project was started with the help of Public Health Service Research Grant AI-01944 from the National Institute of Allergy and Infectious Diseases, which included costs in part of a trip to South America (Levi, 1967). Publication costs were covered in part by the Wetmore-Colles Fund.

TAXONOMIC SECTION

Molinaranea Mello-Leitão

Type species. Molinaranea molinai Mello-Leitão, 1940: 238 (=*Molinaranea magellanica* Walckenaer). It is the only species in the genus cited by Mello-Leitão. The generic name is feminine.

Diagnosis. As in *Eriophora,* but not in *Parawixia,* the scape originates from the anterior of the epigynum and bends over itself to point posteriorly (Figs. 4–6, 40–42). The epigynum has a cavity on each side under the scape (Figs. 4, 5), with the floor of the cavity continuing posteriorly to form the posterior median plate (T-shaped in Fig. 6). In contrast, the posterior median plate of *Eriophora* is small and can be considered the first of the annuli of its scape (Levi, 1970, figs. 12, 37). In *Parawixia* and *Ocrepeira* the posterior median plate extends anteriorly into the scape (Levi, 1992, figs. 10, 11, 1993, figs. 36, 37, 41, 42).

The palpus has the paramedian apophysis (PM) attached to the conductor (C) and pointing to 7:00 in the left palpus (Figs. 19, 30); the paramedian apophysis is pointed or rounded on its end. The paramedian apophysis lacks the finger that is present in *Parawixia* (Levi, 1992, fig. 7) and the free sclerite that is present in *Eriophora* (Levi, 1970, PM in fig. 4). The embolus (E) of all *Molinaranea* species appears to be distally filiform (Fig. 19, 30), unlike the robust emboli in *Eriophora* (Levi, 1970, fig. 4), *Parawixia* (Levi, 1992, figs. 7, 68), and *Ocrepeira* (Levi, 1993, fig. 32).

Females of *Molinaranea* species differ from *Araneus* females in lacking the distal pocket of the tip of the epigynal scape (Levi, 1991, fig. 1), and in not having the posterior median plate swollen ventrally (Levi, 1991, figs. 1, 2). Males of *Molinaranea* differ from *Araneus* males in having a paramedian apophysis in the palpus (PM in Figs. 19, 30), and the conductor is attached at the top of the sphere formed (behind C in Figs. 19, 30) by the tegulum, not on the edge of the tegulum as in *Araneus* (Levi, 1991, fig. 3). Males differ from most males of *Araneus* in having only one patellar macroseta in the palpus (Fig. 16).

Description. Female. Carapace with pair of indistinct, parallel, dorsal anterior lines (Fig. 1). Carapace usually light in color. Dorsum of abdomen variable in coloration, sometimes green. Venter of abdomen with distinctive color pattern (Figs. 11, 28, 52, 70). Thoracic area 1.5–1.8 times width of cephalic area (Fig. 1). Eyes subequal. Posterior median eyes 0.8–1 diameter apart, 2–5 diameters from laterals (Fig. 1). Median eye quadrangle as wide as long, narrower behind (measured around outside of eyes; Figs. 1, 3). Height of clypeus equals diameter of anterior median eyes

(Fig. 3). Femur shorter than combined patella and tibia (Plate 1D). Abdomen subspherical to oval or triangular, with pair of anterior humps (Figs. 8, 27, 36, 43, 51, 59, 69), sometimes with posterior tubercle (Fig. 59) or pairs of median tubercles (Figs. 7, 8).

Male. Coloration same or darker than in female. Cephalic region of carapace narrower than in females, about half width of thorax (Fig. 14). Eyes subequal. Anterior median eyes are 0.7–1.8 diameters apart, 0.7–2 diameters from laterals. Posterior median eyes 0.6–1 diameter apart, 2.7–5 from laterals. Eye quadrangle resembles that of female (Figs. 14, 16). Height of clypeus 1–2 diameters of anterior median eye (Fig. 16). Lateral eyes on tubercle (Fig. 14). Sternum of *M. magellanica* and *M. clymene* sometimes with pair of macrosetae at the posterior end. Tooth on endite (right of chelicera in Fig. 16). Palpal patella with one macroseta (Fig. 16). Macrosetae on fourth coxa of *M. magellanica* and *M. phaethontis*. Hook on first coxa (at 4:00 in Fig. 16) with corresponding groove on femur of second leg. In *Molinaranea clymene* and *M. magellanica*, ventral faces of all femora have a line of macrosetae, but no two individuals have same length and spacing of macrosetae. *Molinaranea mammifera* and *M. surculora* lack ventral row of setae on first and second femora. In *M. phaethontis* all femora lack ventral setae. Abdomen smaller, same shape as that of female (Figs. 12, 32, 39).

Note. Both Hogg (1913) and Mello-Leitão (1940) described the male and female of *Molinaranea magellanica* as separate species and Mello-Leitão placed them in separate genera as well, the female in *Eriophora* and the male in the new genus *Molinaranea*.

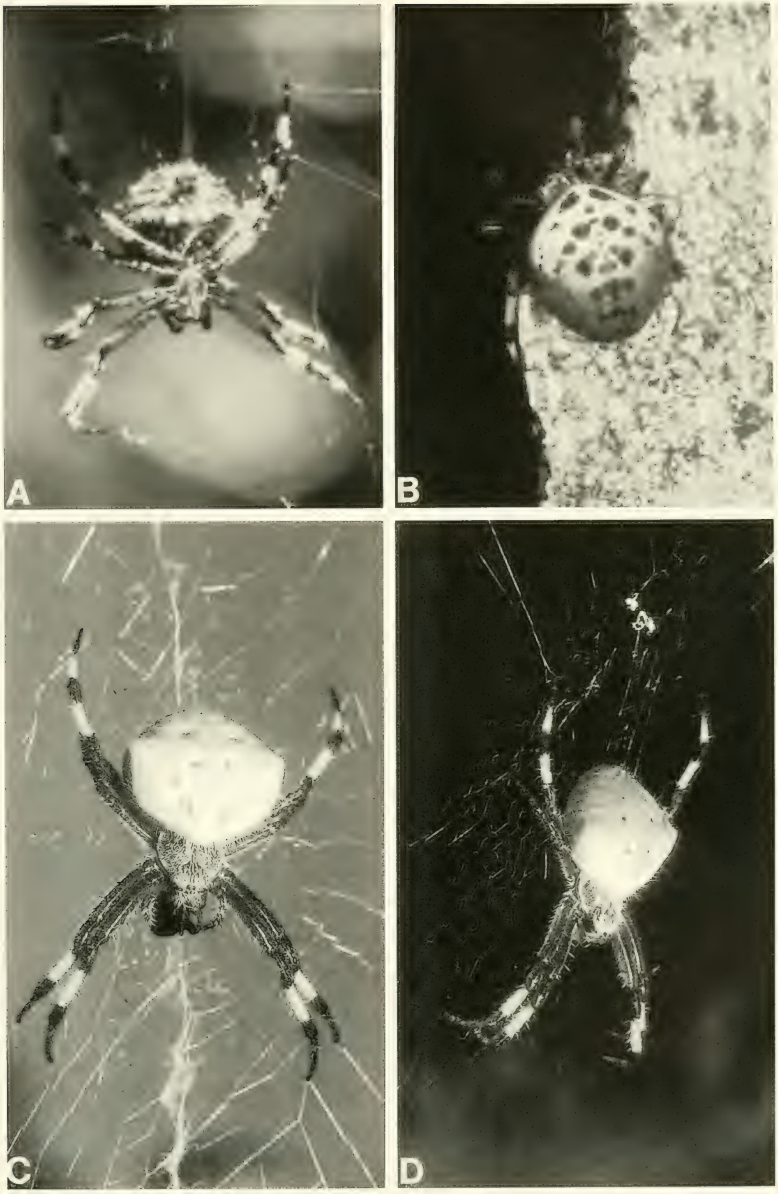
Genitalia. The epigynum may have a long scape (Figs. 4, 5, 33, 34), surpassed in length only by the scape in species of *Eriophora* and *Parawixia* (Levi, 1992, figs. 136, 150). The scape originates from the anterior edge of the base as in *Eriophora*, but unlike *Eriophora* (Levi, 1970, figs. 5, 6) the base of the epigynum is large and has a cavity underneath the scape (Figs. 4, 5, 40, 56).

The paramedian apophysis (PM) of the male palpus is an extension of the conductor, and is pointed or truncate (Figs. 17, 19, 30, 45, 53), not disk-shaped as in *Parawixia* (Levi, 1992, fig. 7) or a separate sclerite as in *Eriophora* (Levi, 1970, fig. 4). The conductor (C) is attached in the middle of the bulb (Fig. 19) as in *Parawixia* (Levi, 1992, fig. 7). In *Eriophora* the conductor has separated from the paramedian apophysis and moved to the edge (Levi, 1970, figs. 2, 3) as in *Araneus* palpi (Levi, 1991, fig. 3). The median apophysis (M) is large, anchored in the radix (R), lacks spines or filaments, and resembles that of *Eriophora, Ocrepeira,* and *Parawixia*. Unlike related genera, the embolus (E) is thread-shaped (Figs. 19, 30, 62, 71). The terminal apophysis (A) is a narrow lobe (at 12:00 in Figs. 17, 19, 30, 38, 45, 53, 62). A subterminal apophysis may be present in the shape of projecting narrow bands (between A and E in Figs. 19, 30).

Relationship. Molinaranea has a paramedian apophysis (PM in Fig. 19) whose pointed or rounded tip is a synapomorphy with that of similar tip found in *Wixia, Pozonia,* and *Ocrepeira* (Levi, 1993, figs. 5a, 23, 32). The unusually long scape of the epigynum and long median apophysis (M) of *Molinaranea* (Figs. 1, 2, 17, 38) are synapomorphies with these structures in *Eriophora* (Levi, 1970, figs. 10, 12) and some *Parawixia* (Levi, 1992, figs. 136, 141) and *Ocrepeira* (Fig. 123; Levi, 1993, fig. 32).

→

Plate 1. (A) *Molinaranea clymene,* coloration, white and browns. (B–D) *Molinaranea magellanica.* (B) Coloration of spider abdomen light green, with dark brown spots. (C, D) Abdomen light green, more yellowish anterior, carapace brown with white setae, legs brown and beige. (C, D, photo credits, R. Preston-Mafham).


A
B
C
D

Additional synapomorphies with these same genera are the attachment of the median apophysis (M) above the radix (R), the proximal sculpturing of the median apophysis at its insertion above the radix, the distal branching of the median apophysis (when present), and the projection of the median apophysis away from the palpal bulb (Figs. 17, 30).

Scharff and Coddington (1997) maintain that the paramedian apophysis attached to the conductor is not homologous with one detached from the conductor. However, the fact that *Molinaranea* has an attached paramedian apophysis, whereas *Eriophora* has a detached one is evidence in favor of the homology between these structures. Similar evidence can be found in *Cyclosa* (Levi, 1999).

Natural History. Most species for which the habitat is known came from wooded portions of the temperate areas, but perhaps this reflects only the preferred habitat frequented by collectors. The orb-web of *Molinaranea* may have a stabilimentum (Plate 1C).

Distribution. Only seven species are known, all from the temperate southern part of South America. One of the largest species (*M. magellanica*) is common at the cold southern tip of the continent, the Strait of Magellan and Tierra del Fuego (Map 1A).

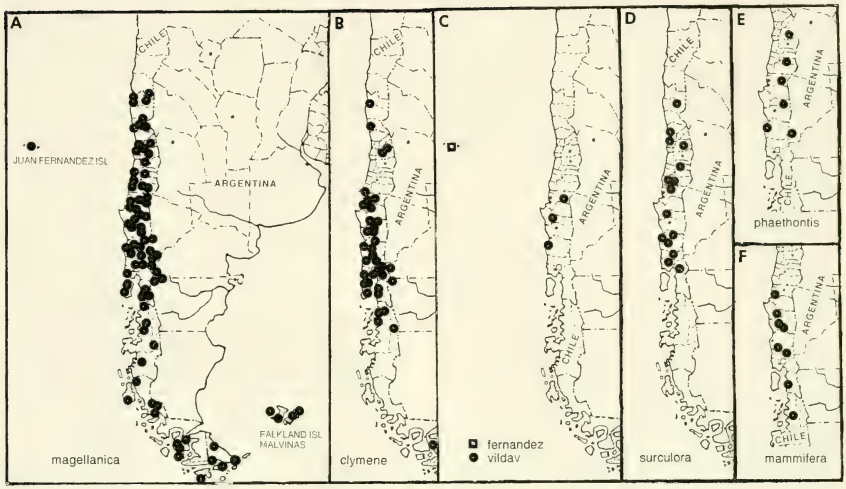
Separating Species. The large genitalia are easy to examine and several species have diagnostic markings on the venter of the abdomen. The dorsal pattern of the abdomen can be quite variable.

KEY TO FEMALE *MOLINARANEA*

1. Venter of abdomen with five black longitudinal lines separated by four white ones (as in Fig. 11) ..... *magellanica*
– Coloration of venter of abdomen otherwise (Figs. 28, 37) 2
2(1). Scape of epigynum not extending beyond posterior margin of base (Fig. 66); length of abdomen about twice its width (Fig. 69) ..... *mammifera*
– Scape of epigynum extending posteriorly beyond base (Figs. 4, 23) 3
3(2). Venter of abdomen with a pair of large white patches (Fig. 28) ..... *clymene*
– Venter of abdomen not marked or marked otherwise (Figs. 37, 44, 52, 60) 4
4(3). Scape of epigynum extending four times the width of the base (Figs. 33, 37) ... *vildai*
– Scape of epigynum at most extending two or three times width of base (Figs. 40, 48, 56) 5
5(4). Scape of epigynum with a constriction (Fig. 56); length of abdomen about one and one half times its width (Fig. 59); tubercles of abdomen large, extended posteriorly (Figs. 59, 61) ..... *phaethontis*
– Scape of epigynum with parallel margins (Figs. 40, 48); length of abdomen equals its width (Figs. 43, 51); tubercles small, extended laterally (Figs. 43, 51) 6
6(5). Posterior median plate of the epigynum with raised septum between scape and posterior median plate (at 12:00 in Fig. 50) ..... *surculora*
– Posterior median plate separated by space from scape (at 12:00 in Fig. 42) .. *fernandez*

KEY TO MALE *MOLINARANEA*

1. Venter of abdomen with five longitudinal black lines separated by four white ones (as in Fig. 11); median apophysis with terminal prong more than twice the length of "upper" prong (Figs. 17, 19, 20, 21) ..... *magellanica*
– Venter of abdomen marked otherwise (Figs. 28, 37); median apophysis prongs otherwise (Figs. 31, 38) 2
2(1) Prongs on tip of median apophysis short, blunt, wider than long, tubercle-like (Figs. 53, 54) ..... *surculora*
– Prong on tips of median apophysis otherwise, pointed (Figs. 31, 38, 46, 63, 72) 3
3(2) Ducts of palpus forming a wide U-shaped structure as in Figure 71 ..... *mammifera*
– Embolus and ducts in palpus straight, never U-shaped (Figs. 29, 38, 45, 62) 4
4(3) "Upper" prong of median apophysis longer than "lower" prong (Figs. 45, 46, 62, 63) 5
– "Upper" prong of median apophysis about same length as "lower" prong (Figs. 30, 31, 38) 6
5(4) Ducts of palpus curved at end (at 12:30 in Fig. 62); conductor (right of curved duct) with large tooth and smaller one (Fig. 62) ..... *phaethontis*
– Ducts of palpus straight (Fig. 45); conductor with small tooth (Fig. 45) ..... *fernandez*
6(4) Venter of abdomen with a pair of white patches (Fig. 28); proximal end of median apophysis with blunt tooth (at 7:00 in Figs. 29, 30) ..... *clymene*
– Venter of abdomen without distinct mark-



Map 1. Distribution of *Molinaranea* species.

ings (Fig. 37); proximal end of median apophysis an enlarged, oval swelling (at 8:00 in Fig. 38) ..... *vildav*

Molinaranea magellanica (Walckenaer), new combination

Plate 1B–D; Figures 1–22; Map 1A

Epeira magellanica Walckenaer, 1847: 467. Specimens from Strait of Magellan, MNHN, lost.

Epeira chilensis Nicolet, 1849: 487. Female from Prov. Valdivia, Chile, MNHN 4102, probably not the holotype, examined. NEW SYNONYMY.

Epeira cinaberina Nicolet, 1849: 490, pl. 5, fig. 9, ♀. Female from central provinces, Santiago, Aconcagua, Chile in MNHN, lost. NEW SYNONYMY.

Epeira flaviventris Nicolet, 1849: 494. Female from Chile (MNHN), lost. Simon, 1884: 121, pl. 3, figs. 2–4, ♀. Simon, 1887: 10, pl. 2, fig. 2, ♀. Simon, 1896: 67. NEW SYNONYMY.

Epeira quadripunctata Nicolet, 1849: 495. Specimen from Chile (MNHN), lost. NEW SYNONYMY.

Epeira obliterata Nicolet, 1894: 496. Specimen from Valdivia (MNHN), lost. NEW SYNONYMY.

Epeira affinis Nicolet, 1849: 498. Immature holotype (?) from Valdivia, Chile, MNHN 3384, examined. NEW SYNONYMY.

Epeira naevia Nicolet, 1849: 499. Specimen from Chile (MNHN), lost. NEW SYNONYMY.

Epeira dorsalis Nicolet, 1849: 499. Specimen from Chile (MNHN), lost. NEW SYNONYMY.

?*Epeira quadrimaculata* Nicolet, 1849: 507. Specimen from Valdivia, Chile, lost. Synonymized with *flaviventris* by Archer, 1963: 25. NEW SYNONYMY.

Araneus flaviventris:—Simon, 1896: 67; Simon 1904: 95. Simon, 1901: 19. Simon, 1904: 95. Tullgren, 1901: 217. Tullgren, 1902: 32. Bonnet, 1955: 503.

Araneus patagonicus Tullgren 1901: 218. Immature holotype from Tweedie, Sierra del Torro [Sierra del Toro, 45°N, 69°W], Patagonia, Argentina, in NRMS, examined. Bonnet, 1955: 563. NEW SYNONYMY.

Araneus vallentini Hogg, 1913: 37, pl. 1, figs. 3a–3e, ♀. Female syntype from Falkland Islands in BMNH, examined. Synonymized with *Araneus cinaberinus* by Schiapelli and Gerschman, 1974: 86. NEW SYNONYMY.

Araneus globiger Hogg, 1913: 39, figs. 4a–4e, ♂. Male syntype from Falkland Islands, in BMNH, examined. Synonymized with *cinaberina* by Schiapelli and Gerschman, 1974: 86. NEW SYNONYMY.

Eriophora wagenknechti Mello-Leitão, 1940: 236, fig. 24, ♀. Female holotype from Juan Fernández Islands in MNRJ, examined. Synonymized with *Araneus cinaberinus* by Schiapelli and Gerschman, 1974: 107. NEW SYNONYMY.

Molinaranea molinai Mello-Leitão, 1940: 238, fig. 25. Male holotype from Juan Fernández Islands (MNRJ), examined. Synonymized with *A. cinaberina* by Schiapelli and Gerschman, 1974: 107. NEW SYNONYMY.

Aranea affinitata Roewer, 1942: 836. New name for

Epeira affinis, Nicolet, preoccupied by *Epeira affinis* Blackwell, 1846. NEW SYNONYMY.
Aranea chilensis:—Roewer, 1942: 839.
Aranea cinaberina:—Roewer, 1942: 839.
Aranea dorsatula Roewer, 1942: 841. New name for *dorsalis* Nicolet, as name preoccupied by *Aranea dorsalis* Fabricius, 1775. NEW SYNONYMY.
Aranea flaviventris:—Roewer, 1942: 842.
Aranea magellanica:—Roewer, 1942: 846.
Aranea naevia:—Roewer, 1942: 848.
Aranea obliterata:—Roewer, 1942: 849.
Aranea patagonica:—Roewer, 1942: 849.
?*Aranea quadrimaculosa* Roewer, 1942: 850. New name for *Aranea quadrimaculata*, which is preoccupied by A. DeGeer, 1778. NEW SYNONYMY.
Aranea quadripunctatula Roewer, 1942: 850. New name for *Aranea quadripunctata*, which is preoccupied by Linnaeus, 1758. NEW SYNONYMY.
Araneus affinis:—Bonnet, 1955: 425.
Araneus chilensis:—Bonnet, 1955: 457.
Araneus cinnaberinus:—Bonnet, 1955, 458. Schiapelli and Gerschman, 1963: 107, 1974: 86.
Araneus dorsalis:—Bonnet, 1955: 498.
Araneus magellanicus:—Bonnet, 1955: 533.
Araneus naevius:—Bonnet, 1955: 548.
Araneus obliteratus:—Bonnet, 1955: 554.
Araneus quadrimaculatus:—Bonnet, 1955: 580.
Araneus quadripunctatus:—Bonnet, 1955: 580.
Parawixia cinnaberina cinnaberina:—Archer, 1963: 24.
Parawixia cinnaberina tigrina Archer, 1963: 24. Male and female syntypes from Prov. Valparaíso, Ventanas, Horcones, Quinteros, Chile, in AMNH, examined. NEW SYNONYMY.

Note. Only the availability and comparison of large collections made it possible to solve numerous synonymies.

Nicolet described and named this species several times, most from specimens 3–5 mm in total length, one-third adult size. For all, he gave the diagnostic character, the ventral abdominal pattern (Fig. 11).

Walckenaer's (1847) description of *Epeira magellanica* was overlooked by Nicolet and also by Tullgren. Simon (1864), who mentions *Epeira magellanica*, did not realize that it is the same species that he, and later Tullgren, called *Epeira flaviventris*. Neither did he recognize that the ventral pattern of the abdomen he illustrated (1884, figs. 2–4) is diagnostic for the species and is also found in specimens from the Strait of Magellan area, the type locality of *Epeira magellanica*.

Simon and Tullgren did not know that some specimens may have a dorsally spotted abdomen, called *cinaberina* by Nicolet (1849, pl. 5, fig. 9; Plate 1B, Fig. 9). This coloration was later used by Archer (1963) as basis for the subspecies *Parawixia cinnaberina tigrina* (*leopardina* might have been more appropriate). This is a color morph, not a subspecies.

A female from Santa Cruz, Chile (MNHN 12473, det. Simon as *cinaberina*) was examined. All specimens determined as *Araneus flaviventris* by Simon in the MNHN are *Molinaranea magellanica*. Also examined was a specimen of *Epeira flaviventris* from Cape Horn, Mision du Cap Horn, 1882–1883, accompanied by a notation that it is the same as chilensis. This specimen was cited by Simon (1896: 67). *Epeira quadrimaculata* was synonymized by Archer (1963), with no reasons given; the synonymy is not convincing. *Epeira chilensis* was erroneously placed in *Metepeira* by Archer (1963).

Bonnet, as for many names, corrected the spelling of *cinaberina* to *cinnaberina*. This is an invalid correction.

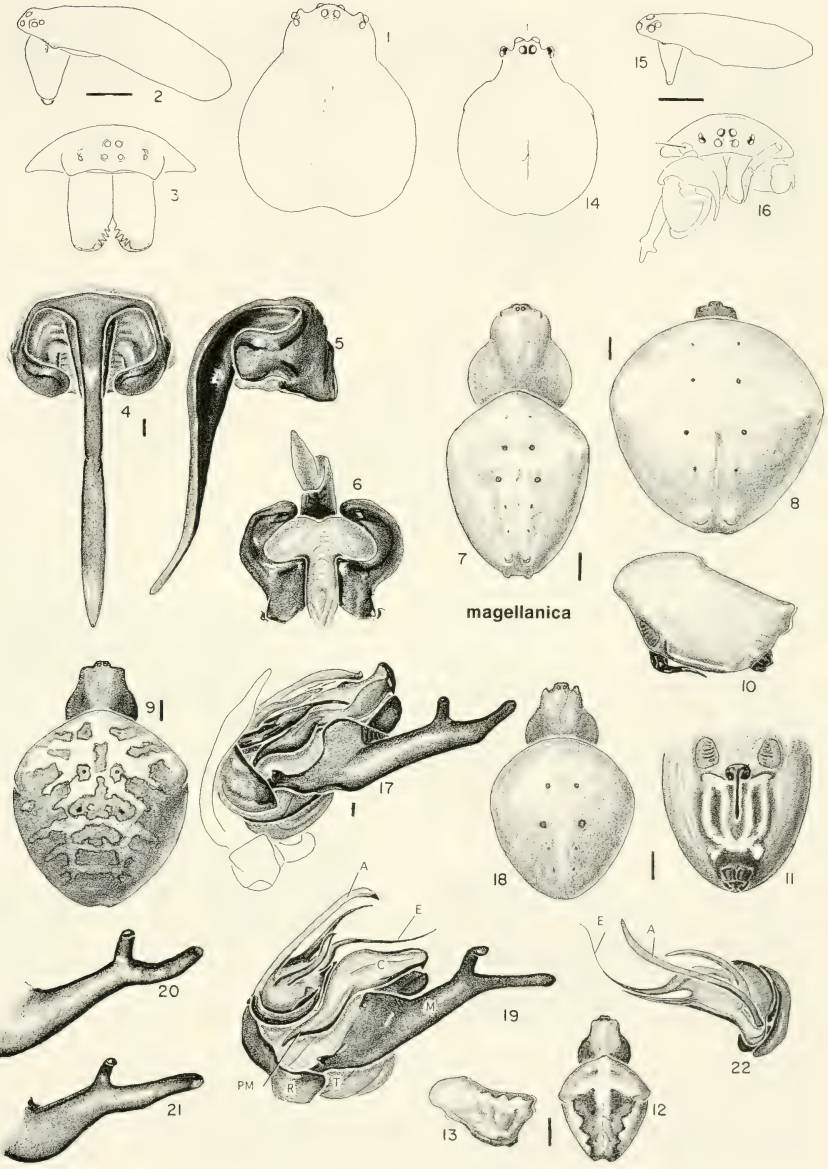
The immature holotype of *Araneus patagonicus* Tullgren is placed here on the basis of the shape of the abdomen and the color pattern of its venter. More recently, both Hogg (1913) and Mello-Leitão (1940)

→

Figures 1–22. *Molinaranea magellanica* (Walckenaer). 1–11, female. 1, carapace. 2, carapace and chelicera. 3, eye region and chelicerae. 4–6, epigynum. 4, ventral. 5, lateral. 6, posterior. 7–9, dorsal. 10, abdomen, lateral. 11, abdomen, ventral. 12, 13, immature. 12, dorsal. 13, abdomen, lateral. 14–22, male. 14, carapace. 15, carapace and chelicera. 16, eye region, chelicerae, and right palpus. 17, left palpus, mesal. 18, dorsal. 19, palpus expanded, mesal. 22, palpus expanded, lateral. 20, 21, median apophysis. 20, (Falkland Islands). 21, (Ñuble, Chile).

Abbreviations: A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; PM, paramedian apophysis; R, radix; T, tegulum.

Scale lines: genitalia, 0.1 mm; others, 1.0 mm.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studied males and females, but neither recognized that they belong together and that this is a widely distributed, previously described, species.

Description. Female from Chillan, Ñuble, Chile. Carapace dark orange (Figs. 7, 8). Chelicerae dark orange, distally brown. Labium, endites orange-brown. Sternum dark brown. Coxae orange and distal leg articles dark orange. Abdomen white dorsally (Figs. 7, 8), green when alive; venter with longitudinal dark lines interspaced by white (Fig. 11). Abdomen with a pair of dorsal tubercles. Total length 9.5 mm. Carapace 4.0 mm long, 3.7 wide in thoracic region, 2.1 behind posterior lateral eyes. First femur 4.5 mm, patella and tibia 5.8, metatarsus 3.4, tarsus 1.3. Second patella and tibia 5.7 mm, third 3.5, fourth 5.2.

Male from Las Cabras, Ñuble Prov., Chile. Coloration darker than in female (Fig. 18); carapace, sternum, coxae, legs orange-brown. Abdomen dorsum greenish white with black folium and a white cardiac patch; venter as in female (Fig. 11). Sternum with two macrosetae on posterior end. Fourth coxae each with one macroseta on one side, the other side with two (1/2), and all femora with a row of ventral macrosetae. Second tibia thicker than first, and with macrosetae. Total length 6.5 mm. Carapace 4.2 mm long, 3.1 wide in thoracic region, 1.2 behind posterior lateral eyes. First femur 3.8 mm, patella and tibia 5.3, metatarsus 3.3, tarsus 2.2. Second patella and tibia 4.6 mm, third 2.7, fourth 4.1.

Note. Males and females have the same ventral pattern on the abdomen (Fig. 11), and are frequently collected together.

Variation. Total length of females 8.0–17.5 mm, males 6.2–9.8. Immatures have the abdomen dorsum with a dark folium (Figs. 12, 13) and have the venter marked as in the adult, and posterior of abdomen with four tubercles (Fig. 13). Females may have the abdomen spotted (Nicolet, 1849, fig. 9; Fig. 9). Few adult females have a dorsal folium pattern on the abdomen, bisected by a median white band (Fig. 7). The abdomen of this species is variable in shape; some poorly fed adults may have four posterior tubercles (Fig. 7), two (Fig. 8), or none.

Of 13 males examined, only 3 (all smaller sized) had sternal macrosetae and these were in variable positions on the posterior of the sternum. Seven had 2/2 macrosetae on the fourth coxae, three had only 1/1 macroseta, and three had 1/2. All had all tarsi with a ventral line of macrosetae, but the number, size, and shape of the macrosetae was variable. For unreliable use of setae counts see Carmichael (1973).

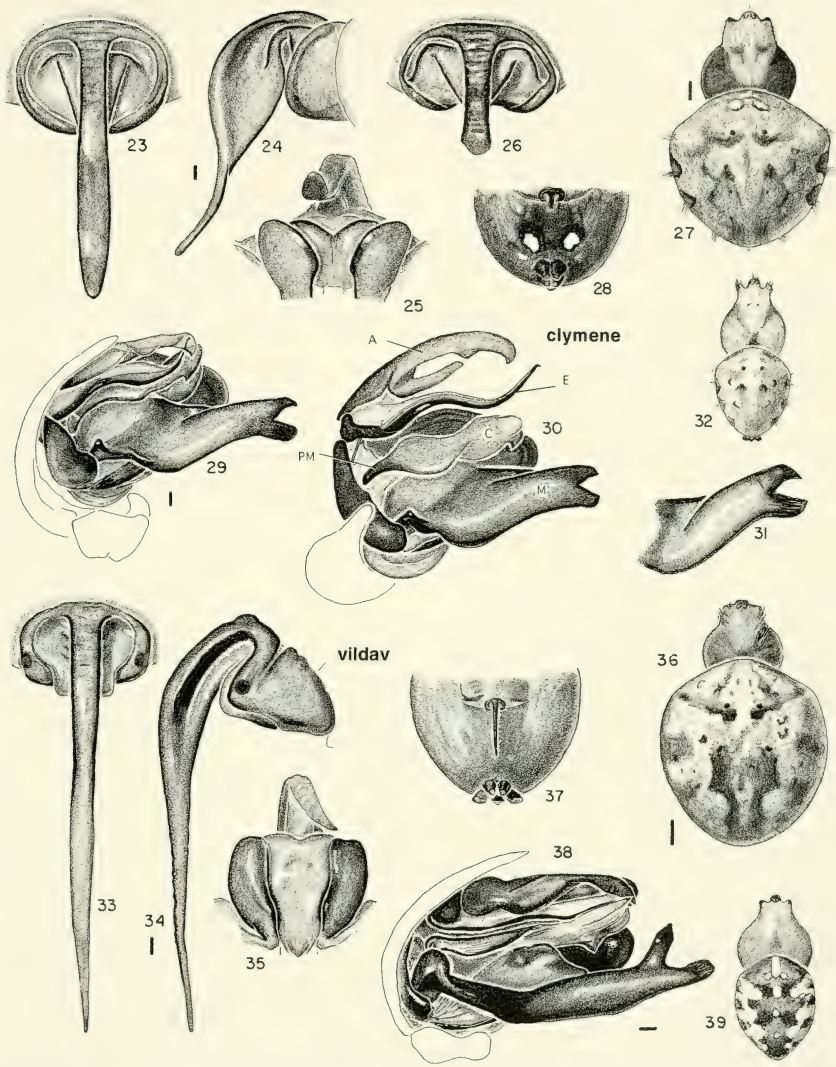
The illustrations were made from Ñuble Province specimens, except Figure 9 from Valparaíso, Figure 18 from W Falkland Island and Figures 12 and 13 from Strait of Magellan region.

Diagnosis. Immatures and adults can be distinguished from other species by the five distinct black, longitudinal stripes on the underside of the abdomen, separated by four white lines (Fig. 11). The epigynum has the rim of the cavities swollen posteriorly, on each side of the scape (Fig. 4). Males have a long median apophysis with two distal prongs, the terminal longest (Figs. 17, 19, 20, 21), but both variable in shape.

Natural History. Found on introduced gorse bushes on Falkland Island; on fence wires at night at El Bolsón; arid coastal scrub in Coquimbo Province; forested sides of swampy brook in Mallenco Province; hotel garden in Villarrica; at 3,500–4,500 m elevation in Codillera de Iquique

→

Figures 23–32. *Molinaranea clymene* (Nicolet). 23–27, female. 23–26, epigynum. 23, ventral. 24, lateral. 25, posterior. 26, ventral with broken scape. 27, dorsal. 28, abdomen, ventral. 29–32, male. 29–31, left palpus, 29, mesal. 30, palpus, expanded, mesal. 31, median apophysis. 32, dorsal.



Figures 33–39. *M. vildav* new species. 33–37, female. 33–35, epigynum. 33, ventral. 34, lateral. 35, posterior. 36, dorsal. 37, abdomen, ventral. 38–39, male. 38, palpus. 39, dorsal.

Abbreviations: A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; PM, paramedian apophysis.

Scale lines: genitalia, 0.1 mm; others, 1.0 mm.

(unknown locality); and in burned forest in Aisén Province.

The vertical orb frequently has a vertical line stabilimentum (Plate 1C).

Specimens Examined. FALKLAND ISLANDS (Islas Malvinas) East Falkland Isl.: Port Darwin, Dec. Jan. 1915, 1916, 4♀ (Phillips Exped., W. S. Brooks, MCZ). West Falkland Isl.: Port Stephens, 5–7 Dec. 1915, 10♀, 1♂ (W. S. Brooks, MCZ). Fitzroy, Stanley, Nov. 1970, 2♀, 1♂ (Rumboll, MACN); West Point Island, Dec. 1971, 1♀ (Rumboll, MACN); New Island, Jan. 1972, 6♀, 2♂ (Rumboll, MACN); Stanley, Dec., 1970, 1♀ (Rumboll, MACN); Puerto San Carlos, Dec. 1971, 8♀ (Rumboll, MACN).

ARGENTINA *Neuquén:* Lago Lácar (several coll., MACN, ZMUC); Pucará, many collections (MACN); Paso del Córdoba, 1200 m, 10 Oct. 1981, 13 imm. (Nielsen, Karsholt, ZMUC); San Martín de Los Andes, 2♀ (MACN, ZMUC); Casa de Piedra, July 1970, 1♀ (MACN); Bariloche, Feb. 1954, 6♀ (M. E. Galiano, MACN); Rahué, 20 Feb 1968, imm. (E. Maury, MACN); Nahuel Huapi, 1960, 4♀ (N. Havrylenko, MACN). *Río Negro:* 1♀ (PAN); El Bolsón (many records, A. Kovács, AMNH); Río Azul, May 1962, 1♀; 5 Dec. 1962, 1♀ (A. Kovács, AMNH); Lago Nahuel Huapi, Puerto Blest, 770 m, 1♀ (Mision Cient. Danesa, ZMUC); SC de Bariloche, Colonia Suiza, 810 m, 20 Dec. 1978, 3♀; 27 Sept. 1981, 1♀ (Mision Cient. Danesa, ZMUC); Lago Frio, 1♀ (MLP); Balmaceda, 27 Jan. 1957, 2♀ (M. Podoceo, MACN); Estancia San Ramón, Río Limay, Rincón Chico, Jan. 1962, 2♀, 1♂ (N. Havrylenko, MACN). *Chubut:* Lago Puelo, El Bolsón, many records (AMNH, ZMUC); El Maiten, 2 Feb. 1966, 1♀; Hoyo de Epuyén, 1958, 2♀; 17 Oct. 1966, 1♀, 1♂; Río Turbio, 12 Jan. 1962, 1♀ (all A. Kovács, AMNH). *Santa Cruz:* Valle Eléctrico, 10–15 Feb. 1949, 1♀ (N. O. Gianolini, MACN). *Tierra del Fuego:* Río Grande, Nov. 1973, 3 imm. (MACN); Estancia Harberton, 25 Jan. 1979, 1♀ (Mision Cient. Danesa, ZMUC); Bahia Aguirre, 12 Nov. 1949, 1♀ (Núñez-Patridge, MACN); Beagle Canal, 1882–1883, 1♀ (Mission du Cap Horn, MNHN). CHILE *Islas Juan Fernández:* Más Afuara, 12 Dec. 1970, 1♀ (O. Solbrig, MCZ); Santa Cruz (MNHN). Very common from about 30° latitude south to Tierra del Fuego.

Molinaranea clymene (Nicolet)
Plate 1A: Figures 23–32; Map 1B

Epeira clymene Nicolet, 1849: 503. Described from Chile. Female holotype in MNHN, lost.

Epeira thalia Nicolet, 1849: 503. Described from Chile. Synonymized by Simon, 1904: 95.

Epeira nigrata Nicolet, 1849: 504. Described from Chile. Synonymized by Simon, 1904: 95.

Epeira inflata Nicolet, 1849: 504. Described from Valdivia, Chile. Synonymized by Simon, 1904: 95.

Epeira erudita Nicolet, 1849: 505. Described from Chile. Synonymized by Simon, 1904: 95.

Epeira hispida Nicolet, 1849: 505. Described from Chile. Synonymized by Simon, 1904: 95.

Epeira valdiviensis Nicolet, 1849: 506. Described from Valdivia. NEW SYNONYMY.

Arancus clymene:—Simon, 1895: 802. Simon, 1904: 95. Bonnet, 1955: 461.

Araneus aysenensis Tullgren, 1902: 32, pl. 3, fig. 4. ♀. Three ♀ syntypes from upper Aysen Valley (Aisén Valley, Coyhaique), Chile in NRMS, examined. Synonymized with *E. clymene* by Simon, 1904: 95.

Aranea aysenensis:—Roewer, 1942: 837.

Aranea valdiviensis:—Roewer, 1942: 855.

Aranea clymene:—Roewer, 1942: 839.

Araneus valdiviensis:—Bonnet, 1955: 626.

Atea erudita:—Archer, 1963: 27.

Note. Simon (1904) did not give reasons for his synonymies. Petrunkevitch (1911) and Roewer (1942) either overlooked or did not accept his synonymy of *aysenensis.* A female in the MNHN, 18529, from Tierra del Fuego, is labeled by Simon as *clymene. Epeira erudita* and *E. valdiviensis* have large white patches on the underside of the abdomen, diagnostic for this species. Of all these names only *A. aysenensis* is adequately described and illustrated. However, I will follow the first reviser, Simon (1904), in the use of the old names.

Description. Female from Concepción Prov., Chile. Carapace light brown with two dark spots on cephalic region, sides of carapace brown (Fig. 27). Chelicerae light brown. Labium, endites light brown. Sternum brown. Coxae light brown, distal leg articles brown with rings indistinctly darker. Abdomen brown, subspherical with a pair of anterior humps (Fig. 27), brown in living individuals. Abdomen with scattered bundles of projecting, white setae (Fig. 27). Abdomen with dorsal folium (Fig. 27), venter black with a pair of prominent white spots (Plate 1A, Fig. 28). Total length 13.0 mm. Carapace 7.0 mm long, 6.1 wide in thoracic region, 3.5 wide in cephalic region. First femur 7.1 mm, patella and tibia 8.2, metatarsus 5.5, tarsus 2.0. Second patella and tibia 7.2 mm, third 5.0, fourth 7.5.

Male. Coloration slightly darker than in

female. Sternum with two macrosetae on posterior tip. Abdomen with bundles of white seate (Fig. 32). Fourth coxae with two macrosetae. All femora with ventral, paired rows of macrosetae. Total length 9.5 mm. Carapace 4.9 mm long, 3.9 wide in thoracic region, 2.0 wide behind posterior lateral eyes. First femur 5.5 mm, patella and tibia 6.9, metatarsus 4.7, tarsus 1.9. Second patella and tibia 5.8 mm, third 3.5, fourth 5.0.

Note. Males and females were matched on the basis of the prominent, ventral pair of white spots on the abdomen in both sexes, and the abdomen covered by tufts of white setae.

Variation. Total length of females 9.5–18 mm, males 7.5–9.8 mm. Photographs of females taken in Valdivia had the abdomen brown, with very distinct white tufts of setae, a lateral wavy margin separating a much darker side. It is common to find females with the epigynal scape broken off (Fig. 26). The illustrations were made from a female from Concepción, and Figure 27 from several specimens and the male from Osorno.

Diagnosis. Females and males can be separated from other species by the pair of white marks on the venter of the abdomen (Fig. 28) and by the bundles of white setae scattered over the abdomen (Figs. 27, 32). Each of the cavities of the base of the epigynum contains a longitudinal, diagonal fold, farthest apart anteriorly, closest together posteriorly (Figs. 23, 26). The rim lacks the swollen posterior region on each side of the scape (Figs. 23, 26), present in *M. magellanica* (Fig. 4). The palpus has a distinctly shaped conductor (at 1:00 in Fig. 29, C in Fig. 30), and the median apophysis has shorter prongs (Figs. 29–31) than those of *M. magellanica* (Figs. 20, 21).

Natural History. Specimens have been collected from a Malaise trap in *Nothofagus* forest in Puyehue, on wet stream bank south of Chaiten, in mixed and wet forest, and in virgin forests in several areas. None of the observed webs had a stabilimentum (Piel, personal communication.)

Specimens Examined. ARGENTINA *Río Negro:* Lago Nahuel Haupi, Puerto Blest, 15 Nov. 1997, 1♀ (Mision Cient. Danesa, ZMUC). *Chubut:* Puerto Blest, 1–6 Jan. 1982, 1♀ (Nielsen, Karsholt, ZMUC). CHILE *Coquimbo:* Elqui, July 1960, 54 imm. (L. Peña, IRSNB). *Aconcagua:* Choapa, E of La Ligua, 27 Sept. 1980, 2 ♀ (L. Peña, AMNH), in the north. Very common, south of the Aisén Valley.

Molinaranea vildav new species
Figures 33–39; Map 1C

Epeira diadema:—Nicolet, 1849: 489. Not *Epeira diadema* Walckenaer [=*Araneus diadematus* (Clerck)], erroneous determination.

Holotype. Female holotype, from Valdivia, Prov. Valdivia, Chile, 15–20 Nov. 1978 (E. Krahmer), in AMNH. The specific name is an arbitrary combination of letters.

Note. Some individuals of this species have a color pattern on the back of the abdomen resembling that of the European *Araneus diadematus* (Figs. 36, 39). Nicolet also noticed the unusually long scape in his Chilean specimens.

Description. Female holotype. Carapace dark orange-brown with white setae (Fig. 36). Chelicerae, labium, endites brown. Sternum orange-brown. Coxae and distal leg articles brown with wide, darker rings. Abdomen dorsum with folium marks, white and brown (Figs. 36, 39); venter gray without distinct marks (Fig. 37). Abdomen spherical with anterior, dorsal pair of humps (Fig. 36). Total length 11 mm. Carapace 3.9 mm long, 3.6 wide in thoracic region, 2.1 wide in cephalic regon. First femur 4.0 mm, patella and tibia 4.6, metatarsus 3.1, tarsus 1.2. Second patella and tibia 4.1 mm, third 2.8, fourth 4.1.

Male from Valdivia, Chile. Coloration as in female but darker (Fig. 39), venter of abdomen black without marks (Fig. 37). Fourth coxae with two macrosetae. Venter of first femur with three macrosetae, third and fourth with a line of ventral macrosetae. Second tibia thicker than first. Abdomen shield-shaped (Fig. 39). Total length 7.4 mm. Carapace 3.9 mm long, 3.7 wide, 1.6 wide behind lateral eyes. First

femur 3.7 mm, patella and tibia 5.0, metatarsus 3.1, tarsus 1.3. Second patella and tibia 4.3 mm, third 3.7, fourth 2.8.

Note. Males and females were collected together.

Variation. Total length of females 7.8–11.0 mm. Illustrations were made from the female holotype and male allotype.

Diagnosis. Molinaranea vildav resembles *M. magellanica* and *M. clymene* in the large size and oval abdomen but can be separated by the unicolored gray venter of the abdomen. In *M. magellanica* the length of the scape projecting beyond the base is about 1.5 times the width of the base (Fig. 4), overhanging length of *M. vildav* scape is more than twice the width of its base (Fig. 33). The scape may extend to the spinnerets (Fig. 37). Unlike the epigynum of the two other species, the posterior median plate is longer than wide with sides almost parallel (center of Fig. 35). The male palpus has the proximal end of the median apophysis with a lobe above the radix and its two terminal prongs are of equal length (Fig. 38); that of *magellanica* has a tooth above the radix and the "lower" prong is longer than the "upper" one (Fig. 19).

Natural History. No data is included on collecting labels.

Specimens Examined. CHILE *Ñuble:* 4 km E Pinto, 5 Jan. 1976, 1♂ (G. Moreno, MCZ). *Malleco:* Sierra Nahuelbuta, 1200 m, W Angol, 23 Jan. 1951, 1♀ (E. S. Ross, A. E. Michelbacher, CAS). *Valdivia:* Valdivia, 8 Dec. 1976, 1♀, 1♂ (E. Krahmer, AMNH).

Molinaranea fernandez new species
Figures 40–47; Map 1C

Holotype. Female holotype, male allotype, and one female paratype, one male and five immature paratypes from Juan Fernandez Islands, Chile, Mas a Tierra, Valle Anson, Plazoleto de Yunque, 200–250 m, Camote side, 1–28 April 1962 (Boris Malkin), in AMNH. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace orange-brown (Fig. 43). Chelicerae, labium, endites, sternum orange. Coxae and distal leg articles orange-brown, with indistinct darker rings. Black line between tips of abdominal tubercles, fading anteriorly, and cut off posteriorly (Fig. 43); venter with indistinct, white square, but no dark markings (Fig. 44). Abdomen subspherical, with a pair tubercles (Fig. 43). Total length 10 mm. Carapace 4.5 mm long, 3.8 wide in thoracic region, 2.3 wide behind posterior lateral eyes. First femur 4.4 mm, patella and tibia 5.4, metatarsus 3.5, tarsus 1.0. Second patella and tibia 4.7 mm, third 2.9, fourth 4.2

Male allotype. Coloration as in female. Abdomen as in female (Fig. 47). Ventrally all femora have a double row of short macrosetae. Total length 7.8 mm. Carapace 4.2 mm long, 3.4 wide in thoracic region, 1.7 wide behind posterior lateral eyes. First femur 4.5 mm, patella and tibia 5.6, metatarsus 4.5, tarsus 1.4. Second patella and tibia 4.8 mm, third 2.7, fourth 3.7.

Note. One of the two males has posterior median eyes that, without staining or dissections, show the parallel rows of cells abutting the canoe-shaped tapetum. Males and females were collected together and have similar distinct coloration.

Diagnosis. Molinaranea fernandez differs from other species by having a distinct transverse dark line between the tubercles of the abdomen, fading out anteriorly and cut off posteriorly (Fig. 43). Unlike other species (except *M. magellanica*), *M. fernandez* has the posterior median plate of the epigynum T-shaped (Fig. 42). The shape of the median apophysis and its prongs, the "upper" one longer than the "lower" one, distinguishes the palpus (Figs. 45, 46). The embolus is embedded in the conductor (at 1:00 in Fig. 45).

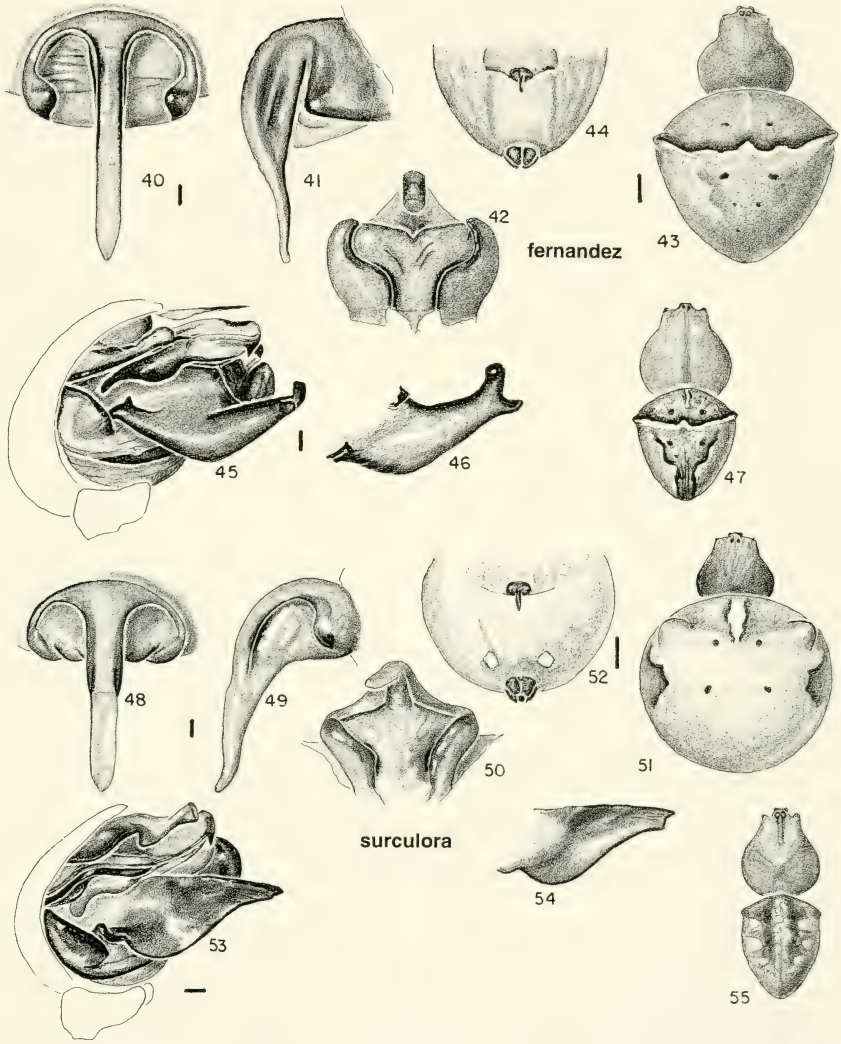
Specimens Examined. No other specimens were found.

Molinaranea surculora (Simon)
Figures 48–55; Map 1D

Araneus surculorum Simon, 1896: 67. Female holotype from Sierra de Chillán [Ñuble Prov.], Chile, in MNHN, examined. Simon, 1904: 96. Bonnet, 1955: 608.

Aranea surculorum:—Roewer, 1942: 853.

Description. Female from Valdivia,



Figures 40–47. *Molinaranea fernandez* new species. 40–44, female. 40–42, epigynum. 40, ventral. 41, lateral. 42, posterior. 43, dorsal. 44, abdomen, ventral. 45–47, male. 45, left palpus. 46, median apophysis. 47, dorsal.

Figures 48–55. *M. surculora* (Simon). 48–52, female. 48–50, epigynum. 48, ventral. 49, lateral. 50, posterior. 51, dorsal. 52, abdomen, ventral. 53–55, male. 53, palpus. 54, median apophysis. 55, dorsal.

Scale lines: genitalia, 0.1 mm; others, 1.0 mm.

Chile. Carapace orange, darkest around border, lightest on anterior half of cephalic region, with many setae. Chelicerae light orange, darker distally. Labium, endites brown. Sternum brown. Coxae light orange; legs brown with indistinct dark rings. Dorsum of abdomen light grayish brown, framed by gray and black margin (Fig. 51); venter slightly dusky between epigynum and spinnerets with a pair of small white pigment spots close to spinnerets (Fig. 52). Abdomen wider than long, anteriorly with a pair of round tubercles (Fig. 51). Total length 7.2 mm. Carapace 3.0 mm long, 2.3 wide in thoracic region, 1.5 wide behind posterior lateral eyes. First femur 2.6 mm, patella and tibia 3.3, metatarsus 2.2, tarsus 1.0. Second patella and tibia 3.3 mm, third 2.1, fourth 3.0.

Male from Valdivia, Chile. Carapace dark orange, anterior of cephalic region lightest. Chelicerae dusky yellow. Labium, endites brown. Sternum dusky brown. Coxae dusky orange, legs brown, indistinctly ringed. Dorsum of abdomen with brown folium (Fig. 55); venter black with pairs of indistinct white spots. Second tibia thicker than first, with prolateral macrosetae. Venter of fourth femur with three macrosetae; others bare. Abdomen longer than wide, with a pair of anterior tubercles (Fig. 55). Total length 5.9 mm. Carapace 3.0 mm long, 2.5 wide in thoracic region, 1.4 wide behind posterior latral eyes. First femur 2.8 mm, patella and tibia 3.5, metatarsus 2.2, tarsus 0.9. Second patella and tibia 3.2 mm, third 1.8, fourth 2.7.

Note. Males and females were collected together.

Variation. Total length of females 5.9–8.8 mm, males 4.3–6.1. Males may have macrosetae on the venter of the third femora. The epigynum illustrated came from a female from Ñuble, the male and female abdomen were from Valdivia, and the palpus was from a specimen from Osorno.

Diagnosis. Immatures can be separated from other species by the wider than long abdomen bearing a pair of tubercles and a dark patch on each side (Fig. 51). In posterior view the epigynum differs from others by the raised septum in the depression between scape and posterior median plate (at 12:00 in Fig. 50). The male differs by the wide, triangular, flat median apophysis having only two small tubercles in place of prongs (Figs. 53, 54).

Natural History. One collecting label records forest as the habitat.

Specimens Examined. CHILE *Limari:* Nague, 20 Sept. 1980, 1♀ (L. E. Peña, AMNH). *Aconcagua:* Zapallar, 27 Nov. 1950. 2♀, 1♂ (E. S. Ross, A. E. Michelbacher, CAS). *Valparaíso:* Valparaíso, 22 Dec. 1973, 1♀ (W. C. Sedgwick, MCZ). *Santiago:* Malleco, Nov. 1979, 1♀ (L. Peña, AMNH). *Curicó:* El Coigo, 1–10 Oct. 1960, ♂ (L. Peña, IRSNB). *Ñuble:* 40 km E San Carlos, 24 Dec. 1950, 1♀ (E. S. Ross, A. E. Michelbacher, CAS); Las Cabras, Dec. 1986, 7♀, 2♂ (L. Umaña, AMNH); Los Lleuques, 5–20 Dec. 1985, 6♀ (L. Umana, AMNH); Cobquecura, 12–14 Feb. 1950, 2♀ (L. E. Peña, IRSNB). *Malleco:* Contulmo, 1909, 1♀ (E. Reimoser, MCZ); El Manzano, nr. Contulmo, 15 Dec. 1985, 1♀, 1♂ (L. E. Peña, AMNH); Nahuelbuta Natl. Park, 12 Oct. 1976, 5♀ (L. E. Peña, AMNH); Sierra Anahuelbuta, W Angol, 1200 m, 23 Jan. 1951, 1♀ (E. S. Ross, A. E. Michelbacher, CAS). *Valdivia:* Santo Domingo, 19 Sep. 1976, 2♂ (E. Krahmer, AMNH); Valdivia, 12 Oct. 1976, 5♀, 2♂; 8 Dec. 1976, 1♀ (E. Krahmer, AMNH, MCZ); Purolón, NW Panguipulli, 10 Jan. 1985, 1♂ (L. E. Peña, AMNH). *Osorno:* Pucatrihue, coast, Jan.–Mar. 1968, 2♀, 1♂ (L. E. Peña, AMNH, MCZ); Pucatrihue, 1–10 Feb. 1980, 1♀ (L. E. Peña, AMNH). *Llanquihue:* Lago Chapo, Dec. 1968, 1♀ (L. E. Peña, MCZ); Los Muermos, 19 Jan. 1951, 1♀ (E. S. Ross, A. E. Michelbacher, CAS).

Molinaranea phaethontis (Simon)
Figures 56–65; Map 1E

Araneus phaethontis Simon 1896: 67. Female holotype from Sierra de Chillán, [Ñuble Prov.], Chile (MNHN), examined. Bonnet, 1955: 565.
Aranea phaethontis: Roewer, 1942: 67.

Description. Female from Valdivia, Chile. Carapace light brown, darkest in center (Fig. 59). Chelicerae, labium, endites, sternum light brown. Coxae, legs light brown, distal leg articles ringed with brown. Abdomen with median, longitudinal, light line flanked by a pair of dark bands, and a light folium posteriorly (Fig. 59); venter with indistinct median, square white patch (Fig. 60). Abdomen with a pair of elongate, dorsal tubercles and a

median posterior extension (Figs. 59–61). Total length 7.5 mm. Carapace 2.5 mm long, 2.2 wide in thoracic region, 1.3 wide in cephalic region. First femur 2.5 mm, patella and tibia 3.0, metatarsus 1.8, tarsus 0.7. Second patella and tibia 2.8 mm, third 1.7, fourth 2.5.

Male from Talca Prov., Chile. Carapace, chelicerae, labium, endites, sternum light brown. Eye region without black pigment. Coxae, legs light brown without dark rings. Dorsum of abdomen with a dark folium (Fig. 64); venter with pair of white patches and a pair of white spots adjacent to the spinnerets (Fig. 65). Fourth coxa with one macroseta. Second tibia thinner than first, with few macrosetae. Abdomen oval (Fig. 64). Total length 5.3 mm. Carapace 2.3 mm long, 2.0 wide, 0.9 wide behind lateral eyes. First femur 2.6 mm, patella and tibia 3.5, metatarsus 2.0, tarsus 0.9. Second patella and tibia 2.9 mm, third 1.7, fourth 2.5.

Note. Males and females were matched by elimination and by their similar coloration.

Variation. Total length of females 5.5–8.2 mm, males 5.3–5.7. Illustrations were made from a female from Valdivia and male from Talca.

Diagnosis. Females and immatures may be distinguished from others by the shape of the abdomen, elongate with two long, pointed tubercles (Figs. 59, 61). Females are also distinguished by having a constriction of the scape (Fig. 56). The male can be distinguished from other *Molinaranea* by having, the "upper" prong of the median apophysis longer than the "lower" one (Figs. 62, 63), and from *M. fernandez* by the curved tip of the embolus (left of tooth at 1:00 of Fig. 62).

Specimens Examined. ARGENTINA *Neuquén:* Lago Lacar, Pucará, 10 Nov. 1978, 1♂ (Mision Cient. Danesa, ZMUC). CHILE *Metropolitana:* El Manzano, Santiago, 13 Oct. 1982, 1♂ (L. E. Peña, AMNH). *Talca:* Andes at Alto de Vilches, 17–24 Oct. 1964, 1♂ (L. Peña, MCZ). *Malleco:* Malalcahuello, 9–15 Dec. 1985, 2♀ (L. E. Peña, AMNH). *Valdivia:* Valdivia, 12 Oct. 1976, 2♀ (E. Krahmer, MCZ).

Molinaranea mammifera (Tullgren) new combination

Figures 66–73; Map 1F

Araneus mammiferus Tullgren, 1902: 34, pl. 3, fig. 5. ♀. Three female syntypes and 10 female paratypes from upper and lower Aysen Valley, [Prov. Aisén], Chile in the NRMS, examined.
Aranea mammifera:—Roewer, 1942: 846.
Araneus mammifer:—Bonnet, 1955: 533.
Lariniacantha mammifera:—Archer, 1963: 26.

Note. Bonnet changed the adjective *mammiferus* to a noun *mammifer* because it had two m's; the adjective has only one m, the noun has two. This is an unacceptable emendation.

Description. Female syntype. Carapace orange-brown with white setae (Fig. 69). Chelicerae brown with orange. Labium, endites brown. Sternum dark brown. Coxae light orange; distal leg articles ringed brown on orange. Abdomen with contrasting dark folium (Fig. 69); venter with a pair of white spots on black, black area with three anterior extensions (Fig. 70). Abdomen elongate with a pair of dorsal humps (Fig. 69). Total length 6.8 mm. Carapace 2.4 mm long, 2.0 wide in thoracic region, 1.2 wide behind posterior lateral eyes. First femur 2.7 mm, patella and tibia 3.1, metatarsus 2.0, tarsus 1.0. Second patella and tibia 2.7 mm, third 1.6, fourth 2.5

Male allotype. Coloration as in female. Abdomen as in female (Fig. 73). Total length 4.6 mm. Sternum, coxae without macrosetae. Third and fourth femora with line of macrosetae on ventral surface. Carapace 2.4 mm long, 1.8 wide in thoracic region, 0.9 wide behind posterior lateral eyes. First femur 3.1 mm, patella and tibia 3.6, metatarsus 2.5, tarsus 2.2. Second patella and tibia 3.0 mm, third 1.8, fourth 2.4.

Note. Males and females were matched on the basis of the similar elongate abdomen (Figs. 69, 73).

Variation. Total length of females 5.8–8.0 mm, males 4.2–5.0. The illustrations were made from a female paratype, and the male from Villarica.

Diagnosis. Immatures can be distinguished from other species by the elongate shape of the abdomen (Fig. 69) with a pair of white spots on the black venter, close to the spinnerets (Fig. 70). Adult females can be separated by the short scape of the epigynum, not extending beyond the posterior of the base (Figs. 66, 67). The palpus of the male differs by the wide U-shaped conductor, (a C lying on its left side in Fig. 71) and the short, wide median apophysis (Figs. 71, 72).

Natural History. Specimens have been found in Valdivian rain forest, by sweeping at dusk at Osorno, in forest in Puyehue, in mixed forest litter in Cautína, and in wet forest in Aisén.

Specimens Examined. CHILE *Concepción:* Ramuntcho, 22 Mar. 1975, 1♀ (T. Cekalovic, MCZ); Hualpen, 3 Nov. 1975, 1♀ (T. Cekalovic, AMNH). *Malleco:* Angol, Cordillera Nahuelbuta, 14–24 Feb. 1977, 1♀ (G. Moreno, AMNH). *Cautín:* 30 km NE Villarrica, Jan. 1965, 1♂ (L. Peña, MCZ); Temuco Cerro Nielo Natl. Park, 300 m, 13 Dec. 1984, 1♀ (S., J. Peck, AMNH). *Valdivia:* 30 km W La Unión, 7–11 Feb. 1988, 1♀ (G. B. Edwards, FSCA). *Osorno:* Termas de Puyehue, 10 Mar. 1965, 1♂ (H. Levi, MCZ); 19–25 Dec. 1982, 1♂ (A. Newton, M. Thayer, AMNH); Parque Nacional Puyehue, 4.1 km E Anticura, 430 m, 19–26 Dec. 1982, 1♂ (A. Newton, M. Thayer, AMNH); Aguas Calientes, Parque Nacional Puyehue, 31 Jan. 1985, 1♀ (N. Platnick, O. Francke, AMNH). *Chiloé:* Chaitén, 1–100 m, 4 Dec. 1981, 1♀ (N. Platnick, R. Schuh, AMNH). *Aisén:* Parque Nacional Río Simpson, 22 km E Aisén, 5 Feb. 1985, 1♀ (N. Platnick, O. Francke, AMNH).

Nicolepeira new genus

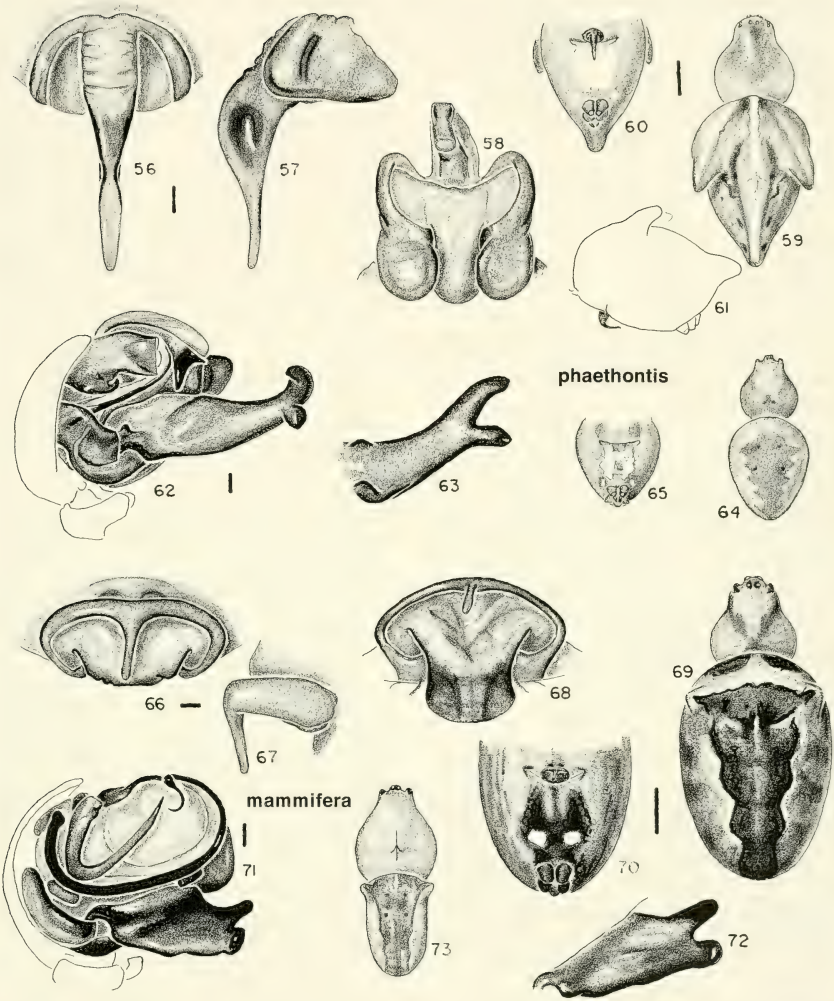
Type species. Epeira flavifrons Nicolet, 1849. The name is an arbitrary combination of letters linking part of author Nicolet's name with epeira. The generic name *Nicolepeira* is feminine.

Diagnosis. The male palpus, unlike that of males of other araneid genera, has a large conductor (C) that covers about one fifth to one third of the bulb, giving the palpus an unusual appearance for an araneid (Figs. 87, 88, 98, 99, 111, 112). Although the conductor is attached in the center of the tegulum, it shows prominently on the lateral side of the palpus (Figs. 88, 99, 112). As in the palpi of *Acacesia, Micrathena,* and *Zygiella* species, but unlike most other araneid palpi, the *Nicolepeira* palpus has a modified sculptured paracymbium (P in Fig. 90; Figs. 88, 89, 99, 112). The epigynum is also unusual for an araneid. Of the three species two have a septum separating paired depressions, with the septum continuing posteriorly into the median posterior plate (Figs. 77, 78, 101, 102). The third species, *Nicolepeira transversalis,* has no septum but has a median soft area bordered posteriorly by the posterior median plate. In two of the species the soft abdomen has tubercles in unusual places for Araneidae (Figs. 79–82, 105–108). The third species has an *Araneus*-like spherical to triangular abdomen (Figs. 94–96) with a pair of anterior, dorsal humps.

Singa and *Hypososinga* might be confused with *Nicolepeira* because of their superficially similar genitalia, but *Singa* and *Hypsosinga* have a shiny, oval, longer than wide abdomen, and are found in the north temperate area, not in South America. The similarities are probably homoplasies.

Description. Females. Small, less than 6 mm in total length, thoracic region of carapace less than 1.6 mm wide. Cephalic region of carapace almost as wide as thoracic region (Figs. 74, 76). Eyes subequal or posterior median eyes slightly larger than anterior medians. Anterior median eyes separated by a distance of 1.5 diameters, and 2–4 diameters from laterals. Posterior median eyes separated by a distance of 1–1.5 diameters, 3–4 diameters from the laterals. Median eyes form a square. Height of clypeus about equal to diameter of anterior median eye. Abdomen soft. In *Nicolepeira transversalis* the abdomen is *Araneus*-like (Figs. 95, 96), in *flavifrons* it is wider than long with two or more anterior lateral tubercles (Figs. 79–82), in *bicaudata* it is longer than wide with two pairs of posterior lateral tubercles (Figs. 105–108). In all three species the shape of the abdomen is variable among individuals (Figs. 79–81, 94, 95, 105–110).

Males. Width of carapace equals that of female. Total length less because of small



Figures 56–65. *Molinaranea phaethontis* (Simon). 56–61, female. 56–58, epigynum. 56, ventral. 57, lateral. 58, posterior. 59, dorsal. 60, abdomen, ventral. 61, abdomen, lateral. 62–65, male. 62, left palpus. 63, median apophysis. 64, dorsal. 65, abdomen, ventral.

Figures 66–73. *M. mammifera* (Tullgren). 66–70, female. 66–68, epigynum. 66, ventral. 67, lateral. 68, posterior. 69, dorsal. 70, abdomen, ventral. 71–73, male. 71, palpus. 72, median apophysis. 73, dorsal.

Scale lines: genitalia, 0.1 mm; others, 1.0 mm.

abdomen (Figs. 106, 113). Cephalic region of carapace wider than half the width of thoracic region (Figs. 83, 85). Eyes subequal or posterior median eyes slightly larger than anterior medians. Anterior median eyes separated by a distance of 1.3–1.5 diameters and 2–5 diameters from laterals. Posterior median eyes separated by a distance of 1–2.2 diameters, 3–5 diameters from laterals (Fig. 83). Height of clypeus about one diameter or less of anterior median eye (Fig. 85). Endite tooth present (at 4:00 in Fig. 85), reduced in *N. transversalis*. Palpal patella with one macroseta (Fig. 85), except no macroseta in *N. transversalis*. No hook on first coxa, no groove on second femur. Second tibia may be thinner than first.

Genitalia. The epigyna lack a scape but may have a flat septum separating the two sides (Figs. 77, 78, 101, 102), or the septum may be lacking (Figs. 91, 92).

The large conductor (C) of the male palpus (Fig. 90) is attached in the middle of the tegulum as in genera in which the palpus has a paramedian apophysis, *Parawixia*, and *Molinaranea*. An unusual, extra sclerite above the radix in *N. flavifrons* (PM center of Fig. 90, at 10:00 in Fig. 87), although it does not have the usual shape of the paramedian apophysis, is probably its homolog.

Relationship. In *N. bicaudata* the abdomen has a laterally biforked posterior end (Fig. 106), as is otherwise found in the American representative of *Molinaranea* (Fig. 8), in *Allocyclosa* (Levi, 1999, fig. 13), *Cyrtophora* (Levi, 1997, fig. 152), and in *Parawixia chubut* (Fig. 117). The biforked tail may be a synapomorphy with *Allocyclosa*, most likely a homoplasy of *Cyrtophora*.

The carapace shape (Figs. 74, 83) is most like that of *Parawixia* (Levi, 1992, figs. 1, 3) probably a synapomorphy.

The septum found in the epigynum (Figs. 77, 78, 101, 102) resembles the scape of *Cyclosa* (Levi, 1999, figs. 31–33). The structure has been lost in *N. transversalis* (Fig. 91) and independently in *Allocyclosa bifurca* (Levi, 1999, fig. 6).

The large conductor (C) embedding an embolic filament (E) (Fig. 90) is probably a synapomorphy with the similar-sized conductor of *Cyclosa* (Levi, 1999, fig. 39). The shape of the sclerite considered the paramedian apophysis (PM in Fig. 90) is most similar in outline to the bar-shaped tip of the *Cyclosa* paramedian apophysis (Levi, 1999, figs. 39, 330), probably a synapomorphy. In *Cyclosa* the median apophysis is partly underneath the conductor (Levi, 1999, M in fig. 39); in *N. flavifrons* the median apophysis is pushed "down" by the conductor (Figs. 88, 90).

The palpi of *Nicolepeira* have an uncommon, sculptured paracymbium (4:00 in Fig. 88, 89; P in Fig. 90). A sculptured paracymbium is found also in *Zygiella* (Fig. 131), *Micrathena* (Levi, 1985, P in fig. 9) and some other araneid genera. I consider these structures homoplasies because, based on other characters, the genera are not related.

The similar cone-shaped palpal tibia of *N. tranversalis* (Figs. 98, 99) and *Zygiella* (Figs. 129, 130) are plesiomorphies.

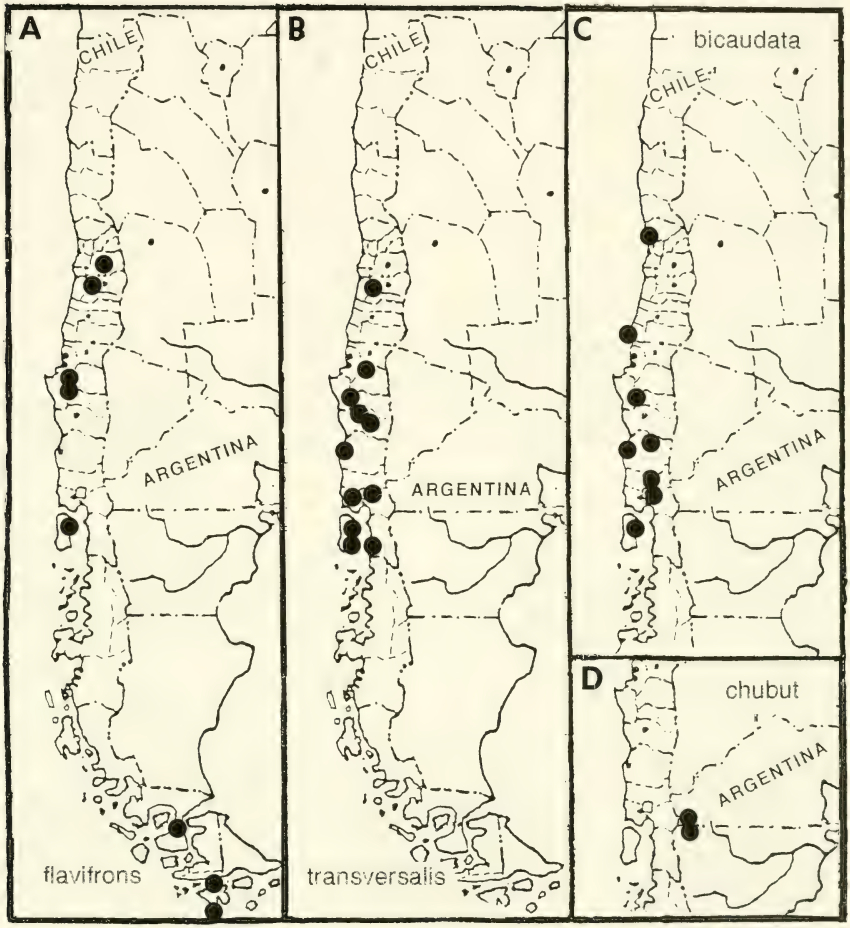
Natural History. Nothing is known of the habits of the three species, except that they are found in shrubby vegetation in woods.

Distribution. Only three species are known, all limited to Chile.

Separating Species. All three species have distinct genitalia and also a variable but distinct shape of the abdomen.

KEYS TO THE SPECIES OF *NICOLEPEIRA*

1. Abdomen usually longer than wide with posterior end forked (Figs. 105–110, 113); male palpus with coiled conductor as in Figures 111 and 112 ..... *bicaudata*
– Abdomen as wide as long (Figs. 95, 100) or wider than long (Figs. 80, 86), conductor curved (Figs. 87, 98, 99) 2
2(1). Abdomen triangular to spherical, as wide as long, with one pair of dorsal humps (Figs. 94–96), epigynum without a septum (Fig. 91); palpus as in Figures 98 and 99, with conical tibia and without patellar macroseta ..... *tranversalis*



Map. 2. Distribution of *Nicolepeira* species and of *Parawixia chubut*.

– Abdomen usually wider than long; that of female with at least two pairs of tubercles (Figs. 79–81); venter with black band enclosing two anterior white spots (Fig. 82); male palpus as in Figures 87–90, with tibia irregular disk-shaped (at 6:00 in Figs. 89, 90), patella with one seta (Fig. 85) ..... *flavifrons*

Nicolepeira flavifrons (Nicolet) new combination
Figures 74–90; Map 2A

Epeira flavifrons Nicolet, 1849: 507, pl. 5, fig. 8, ♀. Female specimens from near Santiago, Chile (MNHN), lost.

Epeira hyadesi Simon, 1884: 121, pl. 3, figs. 5, 6, ♀. Female holotype from Isla Hoste, Orange Bay, [Prov. Antárctica], in MNHN 22346, examined. Simon, 1887: 11, pl. 2, fig. 3, ♀. NEW SYNONYMY.
Araneus hyadesi:—Simon, 1904: 95. Bonnet, 1955: 520.
Aranea flavifrons:—Roewer, 1942: 842.
Aranea hyadesi:—Roewer, 1942: 844.
Araneus flavifrons:—Bonnet, 1955: 503.
Parawixia flavifrons:—Archer, 1963: 25.
Parawixia zigzag Mello-Leitão. This name may be a *nomen nudum* because no description could be found. Specimen from Maullin, Chile, in MNRJ, examined.

Note. Epeira flavifrons is illustrated in Nicolet with two pairs of lateral tubercles, leaving no doubt as to its identity. Simon adequately illustrated the epigynum of *hyadesi*, but apparently did not recognize Nicolet's illustration. Simon's specimen showed only two tubercles on the abdomen. *Epeira hyadesi* is described from a female; the male with this collection (which I erroneously marked lectotype when I examined it in 1988) was apparently added to the collection, sometime in the 19th century, before type specimens were segregated from others.

Description. Female from Punta Arenas, Chile. Carapace brown, eye region lightest, sides of thorax dark brown (Figs. 79, 81). Chelicerae yellow proximally, brown distally. Labium, endites, sternum brown. Coxae and distal leg articles yellow with narrow brown rings. Abdomen white with dorsal, symmetrical dark patches and lines (Figs. 79, 80); venter with narrow black band, anteriorly enclosing a pair of white spots (Fig. 82). Abdomen wider than long, with a pair of large, anterior, dorsal tubercles and three pairs of smaller tubercles (Figs. 79–81). Total length 4.7 mm. Carapace 1.8 mm long, 1.6 wide in thoracic region, 1.3 wide behind posterior lateral eyes. First femur 1.3 mm, patella and tibia 2.0, metatarsus 1.1, tarsus 0.5. Second patella and tibia 1.7 mm, third 0.9, fourth 1.4.

Male from Cordillera Nahuelbuta, Chile. Coloration similar to that of female, legs ringed. Abdomen venter black with one pair of white spots close to genital furrow. Abdomen wider than long (Fig. 86). Palpal patella with one macroseta. Total length 4.7 mm. Carapace 1.7 mm long, 1.7 wide in thoracic region, 1.5 wide behind posterior lateral eyes. First femur 2.0 mm, patella and tibia 2.5, metatarsus 1.7, tarsus 0.7. Second patella and tibia 2.3 mm, third 1.4, fourth 1.7.

Note. Males and females were collected together. Also, they share the white pigment spots on the black ventral band (Fig. 82).

Variation. Total length of females 4.7–6.5 mm, males 4.3–4.7 mm. The shape of the abdomen, number of tubercles, and the shape of the septum of the epigynum are variable. Figures 74–76, 80, 83–85, and 88 came from Dalcahue specimens; the specimen in Fig. 81 came from Ñuble Province. Other illustrations were made from a female from Punta Arenas, and a male from Nahuelbuta.

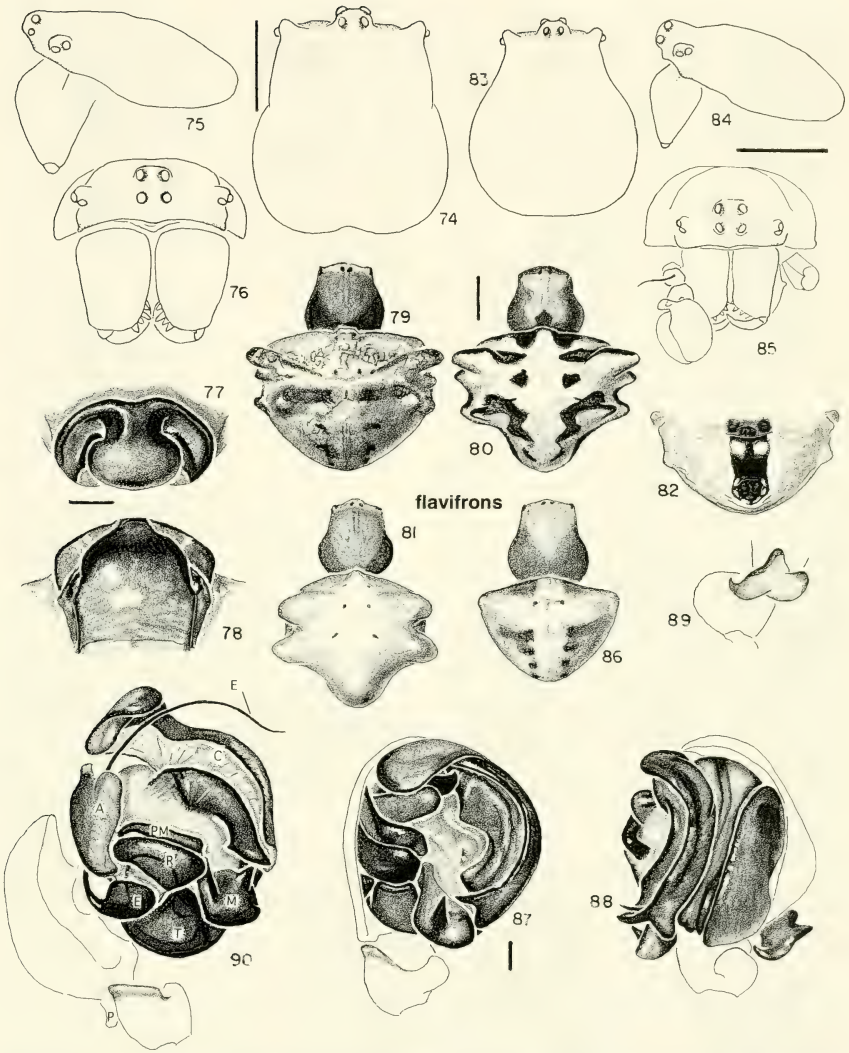
Diagnosis. Females are distinguished from the other two species by having the abdomen wider than long with a variable number of pairs of tubercles on each side (Figs. 79–81), a ventral black band containing an anterior a pair of white spots (Fig. 82), and by the large, round septum of the epigynum (fig. 77). Males have the abdomen wider than long (Fig. 86), the palpus with a large, curved conductor (Figs. 87, 88, 90), and the median apophysis with a long tooth (Figs. 87, 90).

Specimens Examined. CHILE *O'Higgins:* Cachapoal, Las Cabras, 28, 29 Dec. 1986, 1♀ (L. Umaña, AMNH). *Ñuble:* Los Lleuques [?], Dec. 1985, 3♀; Dec. 1986, 1♀ (L. Umaña, AMNH). *Malleco:* Pichinpehuén, Cordillera Nahuelbuta, Jan. 1959, 9♀, 7♂ (L. E. Peña, IRSNB); Butamalal, 1200 m, 26 Jan. 1934, 1♂ (L. E. Peña, IRSNB). *Chiloe:* Dalcahue, 1–4 Apr. 1968, 1♀, 1♂ (L. E. Peña, MCZ). *Magallanes:* Punta Arenas, Quinta Pillet, 14 Jan. 1966, 1♀, 1♂; 26 Feb. 1969, 2♀ (T. Cekalovic, MCZ).

Nicolepeira transversalis (Nicolet), new combination

Figures 91–100; Map 2B

Epeira transversalis Nicolet, 1849: 493. Males and females from Chile in MNHN, lost (?). Simon, 1864: 263.



Figures 74–90. *Nicolepeira flavifrons* (Nicolet). 74–82, female. 74, carapace. 75, carapace and chelicera. 76, eye region and chelicerae. 77, 78, epigynum. 77, ventral. 78, posterior. 79–81, dorsal. 82, abdomen, ventral. 83–90, male. 83, carapace. 84, carapace and chelicera. 85, eye region, chelicerae, and right palpus. 86, dorsal. 87, left palpus, mesal. 88, palpus, ventral. 89, paracymbium. 90, palpus, expanded, mesal.

Abbreviations: A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; PM, paramedian apophysis; R, radix; T, tegulum.

Scale lines: genitalia, 0.1 mm; others, 1.0 mm.

Aranea transversalis:—Roewer, 1942: 854.
Araneus transversalis:—Bonnet, 1955: 613.
Neosconella transversalis:—Archer, 1963: 28.

Note. Nicolet's description fits this species.

Description. Female holotype. Carapace yellowish, dusky brown on sides, in center underlain by white pigment; white setae on sides (Fig. 94). Chelicerae orange. Labium, endites dusky brown. Sternum dark brown. Coxae yellow. Distal articles of legs yellowish with dusky rings. Dorsum of abdomen white with anterior transverse dark band and pairs of black patches posteriorly (Figs. 94, 95); venter with dusky band from pedicel to behind spinnerets (Fig. 97). Abdomen as wide as long, with a pair of anterior, dorsal tubercles (Figs. 94–96). Total length 4.5 mm. Carapace 1.7 mm long, 1.6 wide, 0.9 wide behind eyes. Total length 3.4 mm. Carapace 1.6 mm long, 1.3 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.9 mm, patella and tibia 2.4, metatarsus 1.4, tarsus 0.5. Second patella and tibia 2.0 mm, third 1.1, fourth 1.7.

Male from Ensenada, Chile. Carapace dusky yellow, in center underlain by white pigment. Chelicerae, labium, endites, sternum brown. Coxae yellow; distal leg articles yellow with light brown rings. Dorsum of abdomen white with tiny black spots, venter with a median dusky band from pedicel to and including spinnerets. Palpal patella without macrosetae. Palpal tibia cone-shaped (Figs. 98, 99). Total length 2.9 mm. Carapace 1.5 mm long, 1.3 wide in thoracic region, 0.7 wide behind posterior lateral eyes. First femur 1.9 mm, patella and tibia 2.4, metatarsus 1.6, tarsus 0.5. Second patella and tibia 1.9 mm, third 0.9, fourth 1.4.

Note. Males and females were collected together.

Variation. Total length of females 3.5–5.5 mm, males 2.9–3.5. Figures 91–93 illustrate specimens from Las Cabras; Figure 94 specimen from Isla Teja; Figure 95 specimen from Ñuble Province; and Figures 98–100 a male from Villarrica.

Diagnosis. Females are distinguished by having the abdomen about as long as wide with one pair of humps (Figs. 94–97). The epigynum is without septum and without scape (Fig. 91), and the posterior median plate of the epigynum is triangular (Fig. 92). Males differ by the shape of median apophysis (center in Fig. 98) and conductor of the palpus (at 3:00 in Fig. 98), and the wide diagonal sclerite (between 2:00 and 10:00 in Fig. 99).

Natural History. Specimens were collected in *Podocarpus* association, at Los Muermos.

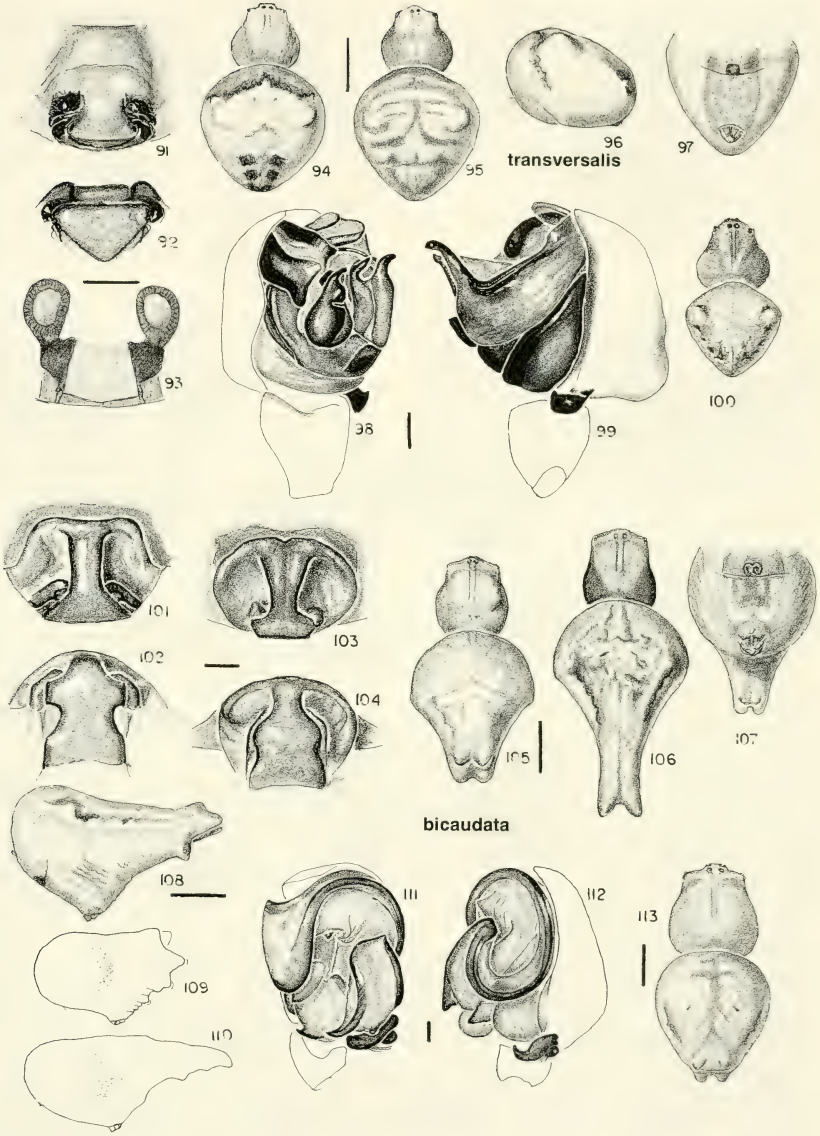
Specimens Examined. CHILE *Ñuble:* Los Lleuques [?], 5–20 Dec. 1985, 2♀ (L. Umaña, AMNH). *Cachapoal:* Las Cabras, 26–28 Dec. 1986, 2♀ (L. Umaña, AMNH). *Bío-Bío:* 5 km W Tucapel, 28 Dec. 1950, 2♀ (E. S. Ross, A. E. Michelbacher, CAS). *Malleco:* Contulmo, 1909, 1♀ (E. Reimoser, MCZ). *Cautín:* Villarrica, 27–28 Feb. 1979, 1♂ (L. E. Peña, AMNH); Chacamo, W Temuco, NW of Nueva Imperial, 17–23 Feb. 1981, 1♂ (L. E. Peña, AMNH). *Valdivia:* Huachocopihue, 7 Mar. 1965, 1♂ (H. Levi, MCZ); Isla Teja, 6 Mar. 1965, 2 imm., 1♀, 2♂ (H. Levi, MCZ). *Llanquihue:* 2–3 km NW Ensenada, 18 March 1965, 1♂ (H. W. Levi, MCZ); 4 km S Los Muermos, 170 m, 12 Nov. 1966, 1♀ (M. E. Irwin, E. I. Schlinger, CAS). *Chiloe:* Isla de Chiloé, Pta. Carmen, Quellón, 15–19 Mar. 1981, 1♀ (L. E. Peña, AMNH); Dalcahue, 1–4 Apr. 1968, 1♀ (L. E. Peña, MCZ). *Palena:* Chaitén, Dec. 1985, 2♀ (L. E. Peña, AMNH).

→

Figures 91–100. *Nicolepeira transversalis* (Nicolet). 91–97, female. 91–93, epigynum. 91, ventral. 92, posterior. 93, cleared, dorsal. 94, 95, dorsal. 96, abdomen, lateral. 97, abdomen, ventral. 98–100, male. 98, 99, left palpus. 98, mesal. 99, ventral. 100, dorsal.

Figures 101–113. *N. bicaudata* (Nicolet). 101–110, female. 101–104, epigynum. 101, 103, ventral. 102, 104, posterior. 105, 106, dorsal. 107, abdomen, ventral. 108–110, abdomen, lateral. 111–113, male. 111, palpus, mesal. 112, palpus, ventral. 113, dorsal.

Scale lines: genitalia, 0.1 mm; others, 1.0 mm.


91
92
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transversalis
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Nicolepeira bicaudata (Nicolet), new combination

Figures 101–113; Map 2C

Epeira carenata Nicolet, 1849: 509. Female from Valdivia, in MNHN lost. NEW SYNONYMY.
Epeira bicaudata Nicolet, 1849: 510, pl. 5, fig. 11, ♀. Specimens came from Chile. Simon, 1864: 263.
Aranea bicaudata:—Roewer, 1942: 837.
Aranea carenata:—Roewer, 1942: 838.
Araneus bicaudatus:—Bonnet, 1955: 442.
Araneus carenatus:—Bonnet, 1955: 452.

Note. The shape of the abdomen matches Nicolet's description of *E. carenata.* However, the name *bicaudata* is used because its female was illustrated by Nicolet.

Description. Female from Putatrihue, Chile. Carapace orange-brown, sides of thorax dark brown (Fig. 106). Chelicerae, labium, endites brown. Sternum dark brown. Coxae and distal leg articles light brown; distal articles ringed. Abdomen white, gray, and black with irregular patches (Figs. 105, 106); venter gray with pair of small, indistinct light patches in front of spinnerets (Fig. 107). Abdomen with a pair of dorsolateral tubercles and two pairs of posterior tubercles on an extension (Figs. 105–107). Total length 6.1 mm. Carapace 1.9 mm long, 1.5 wide in thoracic region, 1.3 wide behind posterior lateral eyes. First femur 1.7 mm, patella and tibia 2.3, metatarsus 1.3, tarsus 0.7. Second patella and tibia 1.8 mm, third 1.1, fourth 1.3

Male from Dalcahue. Coloration lighter than in female. Abdomen with specks of white, venter as in female. Palpal patella with one macroseta. Second, tibia thinner than first, not modified. Abdomen with four posterior tubercles (Fig. 113). Total length 5.1 mm. Carapace 2.3 mm long, 1.8 wide in thoracic region, 1.4 wide behind posterior lateral eyes. First femur 2.5 mm, patella and tibia 3.4, metatarsus 2.0, tarsus 0.7. Second patella and tibia 2.5 mm, third 1.3, fourth 1.9.

Note. The only male found, the one described, is lightly sclerotized and may be freshly molted (Figs. 111–113). Males and females were matched by elimination and on the basis of the male's similarly shaped abdomen (Fig. 113).

Variation. Total length of females 4.9–6.2 mm. The posterior extension of the abdomen is variable (Figs. 105–110). Figures 101, 102, 106, 109, and 110 were made from specimens from Malleco; Figures 107 and 108 from specimens from Putatrihue; Figures 111–113 from specimens from Dalcahue. The carapace of the only male seems slightly larger than that of the female (Fig. 113).

Diagnosis. The female is distinguished from other species by the unusual shape of the abdomen: one or two pairs of terminal, side by side tubercles and the concave sides of the posterior of the abdomen (Figs. 105, 106). Unlike *N. flavifrons* (Fig. 77) *N. bicaudata* has the septum of the epigynum longer than wide (Figs. 101, 103). The abdomen of the male is similar to that of the female, and the enormous conductor of the palpus covers most of the palpal bulb except for an S-shaped area (Fig. 111).

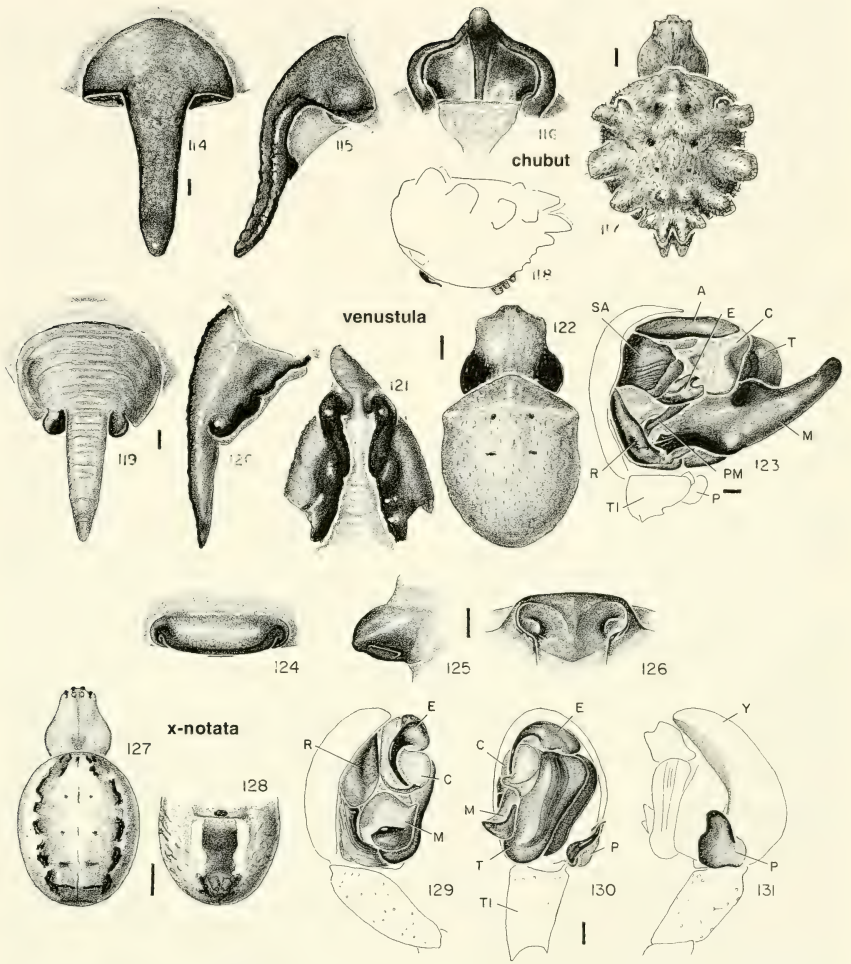
Specimens Examined. CHILE *Petorca:* Zapallar, 27 Nov. 1950, 1♀ (E. S. Ross, A. E. Michelbacher, CAS). *Santiago:* Q. Córdoba, coast, 15–20 Feb. 1979, 1♀ (L. E. Peña, AMNH). *Cauquenes:* Cobquecura, Tregualemu, 31 Dec. 1958, 1♀; 12–18 Feb. 1954, 1♂ (L. E. Peña, IRSNB). *Ñuble:* Los Lleuques [?], 5–20 Dec. 1985, 1♀ (L. Umána, AMNH). *Malleco:* El Manzano, nr. Contulmo, 15 Dec. 1985, 1♀ (L. E. Peña, AMNH); Puren Contulmo Natur. Mon., mixed evergreen forest, 13 Feb. 1985, 1♀ (S., J. Peck, AMNH). *Valdivia:* Purolón, NW Panguipulli, 10 Jan. 1985, 1♀ (L. E. Peña, AMNH). *Osorno:* Putatrihue, 12 Apr. 1968, 1♀ (L. E. Peña, MCZ). *Llanquihue:* Ensenada, 1 Dec. 1988, 1♀ (V. D., B. Roth, CAS). *Chiloe:* Dalcahue, 15 Feb. 1954, 1♂ (L. E. Peña, IRSNB).

Parawixia chubut new species

Figures 114–118; Map 2D

Holotype. Female holotype from El Hoyo, Chubut, Argentina, 10 Jan. 1962 (A. Kovács) in AMNH. The specific name is a noun in apposition after the locality.

Description. Female holotype. Carapace, chelicerae, labium, endites, sternum dark brown. Coxae and distal leg articles dark brown. Abdomen dark brown with



Figures 114–118. *Parawixia chubut* new species, female. 114–116, epigynum. 114, ventral. 115, lateral. 116, posterior. 117, dorsal. 118, abdomen, lateral.

Figures 119–123. *Ocrepeira venustula* (Keyserling). 119–122, female. 119–121, epigynum. 119, ventral. 120, lateral. 121, posterior. 122, dorsal. 123, male, left palpus.

Figures 124–131. *Zygiella x-notata* (Clerck). 124–128, female. 124–126, epigynum. 124, ventral. 125, lateral. 126, posterior. 127, dorsal. 128, abdomen, ventral. 129–131, male palpus. 129, mesal. 130, ventral. 131, lateral with shaded paracymbium.

Abbreviations: A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; P, paracymbium; PM, paramedian apophysis; R, radix; SA, subterminal apophysis; TI, tibia; Y, cymbium.

Scale lines: genitalia, 0.1 mm; others, 1.0 mm.

tiny brownish-white spots and symmetrical black patches (Fig. 117); venter without distinct marks. Eyes subequal. Anterior median eyes 1 diameter apart, 2.2 diameters from laterals. Posterior median eyes 1.2 diameters apart. Ocular trapezoid wider than long, widest in front. Height of clypeus equals 1.7 diameters of anterior median eye. Abdomen with four pairs of lateral tubercles, four pairs posterior, and one anterior median. Total length 12.0 mm. Carapace 5.1 mm long, 4.5 wide in thoracic region, 2.3 wide behind posterior lateral eyes. First femur 4.0 mm, patella and tibia 5.6, metatarsus 3.1, tarsus 1.4. Second patella and tibia 5.1 mm, third 2.9, fourth 4.7.

Variation. Total length of females 11.5–12.0 mm. The illustrations were made from the female holotype.

Diagnosis. The large and long tubercles of the abdomen distinguish *P. chubut* from other *Parawixia* species. The epigynum (Figs. 114–116) has a relatively long scape and a transverse posterior median plate.

Natural History. The specimens from El Bolsón (Feb. 1961) were collected from a wire fence at night.

Specimens Examined. ARGENTINA *Río Negro:* El Bolsón, 1958, 1♀; 1 Feb. 1961, 8♀, 14 imm.; 27 Sept. 1961, 4 imm. (all A. Kovács, AMNH). *Chubut:* El Hoyo, 1958, 1♀, 1 imm. (A. Kovács, AMNH). CHILE *Cautín:* Río Huachitivo [?], 12 Feb. 1981, 1♀ (T. Cekalovic, AMNH).

Ocrepeira venustula (Keyserling) Figures 119–123

Epeira venustula Keyserling, 1880: 308, pl. 4, fig. 11, ♀. Female holotype from Nova Friburgo, Est. Rio de Janeiro, Brazil, in the L. Koch collection, lost.

Araneus albisecta Mello-Leitão, 1936: 127, pl. 15, ♀. Female holotype from Papudo, [Prov. Petorca], Chile (MNRJ), lost. Bonnet, 1955: 127. NEW SYNONYMY.

Aranea albisecta:—Roewer, 1942: 886.

Molinaranea albisecta:—Levi, 1991: 177. Platnick, 1993: 451.

Ocrepeira venustula:—Levi, 1993: 94, figs. 29–33, 143–154, ♀, ♂.

Note. Mello-Leitão's illustration of *A. albisecta* is recognizable.

Description. Female from Angol, Chile. Carapace brown, with white setae, sides dark brown (Fig. 122). Chelicerae, labium, endites dark brown. Sternum uneven brown. Coxae and distal leg articles brown with indistinct darker rings. Abdomen brown with a transverse white line between two tubercles (Fig. 122); area anterior of white line darker than area posterior of line; venter brown. Abdomen with a pair of dorsal tubercles (Fig. 122). Total length 9.3 mm. Carapace 4.3 mm long, 3.5 wide in thoracic region, 2.3 wide in cephalic region. First femur 3.6 mm, patella and tibia 4.8, metatarsus 3.0, tarsus 1.3. Second patella and tibia 4.4 mm, third 3.6, fourth 4.8.

Male from Ñuble, Chile. Coloration lighter than that of female. Carapace, sternum, coxae, light brown. Distal leg articles light brown, ringed darker brown. Abdomen with gray folium and brown tips of humps, venter gray with an indistinct pair of white patches in front of spinnerets. Ocular quadrangle square. Clypeus height equals 1.8 diameters of anterior median eye. Endite with tooth. Palpal patella with one macroseta. First coxa with hook. Third and fourth coxa and trochanter each with one short macroseta. Femora, except third, with a line of short, ventral macrosetae. Abdomen as in female. Total length 5.0 mm. Carapace 4.1 mm long, 3.6 wide in thoracic region, 1.6 wide behind posterior lateral eyes. First femur 3.8 mm, patella and tibia 4.8, metatarsus 3.0, tarsus 1.0. Second patella and tibia 3.9 mm, third 2.7, fourth 3.9.

Variation. Total length of females 7.3–9.3 mm, males 5.0–8.3 mm. The illustrations are of a female from Angol and the male from Pinto.

Diagnosis. The scape beyond the base of the epigynum is about as long as the length of the base (Fig. 119). The shape of the large median apophysis distinguishes the male from others (Fig. 123).

Records. CHILE *Elqui:* La Serena, Feb. 1947, 1♂ (M. Pino, AMNH); 50 km S La Serena, Dec. 1950, 1♂ (E. S. Ross, A. E. Michelbacher, CAS). *Choapa:* El Bato, E of Illapel, 10 Oct. 1985, 1♂ (L. E. Peña,

AMNH). *San Felipe:* Putaendo, 28 Nov. 1981, 2♀ (M. Pino, AMNH). *Region Metropolitana:* San Manuel, S of Melipilla, 6–8 Dec. 1980, 1♂ (L. E. Peña, AMNH). *Talca:* 35 km N Talca, 22 Dec. 1950, 1♀ (E. S. Ross, A. E. Michelbacher, CAS). *Concepción:* Escuadrón, 11 Nov. 1979, 1♂ (T. Cekalovic, AMNH). *Ñuble:* 4 km E Pinto, 5 Jan. 1976, 1♂ (G. Moreno, MCZ). *Malleco:* Angol, 29 Jan. 1951, 6♀, 2♂ (E. S. Ross, A. E. Michelbacher, CAS). *Cautín:* 16 km NE Pucón, 12 Jan. 1951, 1♀ (E. S. Ross, A. E. Michelbacher, CAS).

Zygiella x-notata (Clerck) Figures 124–131

Araneus x-notatus Clerck, 1758: 46, pl. 2, fig. 5. A Clerck specimen bearing this name in NRMS, not examined.

Zilla bösenbergi Keyserling, 1878: 575, pl. 14, figs. 4, 5, ♀, ♂. Female and male syntypes from Uruguay in BMNH. Synonymized by Levi, 1974.

Larinia maulliana Mello–Leitão, 1951: 331, figs. 5, 6, ♂. Male holotype from Maullín, Chile. Synonymized by Levi, 1974.

Zygiella x-notata:—Levi 1974: 276, figs. 21–31, 57, 58, ♀, ♂.

Description. Female from Peulla, Llanquihue, Chile. Carapace orange (Fig. 127). Chelicerae, labium, endites, sternum orange. Coxae and distal leg articles orange, ringed brown. Abdomen white with dorsal dark patches and lines, forming a large oval (Fig. 127); venter with median black band bordered by white band on sides (Fig. 128). Eyes subequal. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes 0.8 diameter apart, 1.5 diameters from laterals. Ocular trapezoid square. Height of clypeus equals 0.6 diameter of anterior median eye. Abdomen oval, widest in middle, without tubercles (Fig. 127). Total length 6.9 mm. Carapace 2.6 mm long, 2.2 wide in thoracic region, 1.4 wide behind posterior lateral eyes. First femur 3.4 mm, patella and tibia 4.3, metatarsus 3.2, tarsus 0.1. Second patella and tibia 3.2 mm, third 1.85, fourth 2.6.

Male from Llanquihue Prov., Chile. Coloration slightly darker than in female. Eye sizes and spacing as in female. Clypeus height 0.8 diameter of anterior median eye. Endite with tooth, faced by a tubercle on palpal trochanter. Palpal tibia cone-shaped (Figs. 129–131), patella with one macroseta. First coxa without hook. Second tibia thicker than first. Abdomen as in female. Total length 5.5 mm. Carapace 3.0 mm long, 2.4 wide in thoracic region, 1.3 wide behind posterior lateral eyes. First femur 3.6 mm, patella and tibia 5.7, metatarsus 5.0, tarsus 0.9. Second patella and tibia 3.3 mm, third 2.0, fourth 2.8.

Note. The illustrations were made from specimens from Llanquihue Prov., Chile.

Diagnosis. The coloration, abdomen widest in middle (Figs. 127, 128), and the slightly projecting epigynum distinguish females (Figs. 124–126); the palpal structure and cone-shaped tibia (Figs. 129–131) distinguish males.

Palpal Structure. The cone-shaped palpal tibia (TI in Figs. 129–131) has numerous trichobothria. The paracymbium (P in Figs. 130, 131) is modified into a plate. The saberlike embolus (E) lies on the conductor (C). The conductor (C) of *Zygiella* is attached to the edge of the tegulum (T in Fig. 130). The round median apophysis (M) is attached "below" the radix (R in Fig. 129) and does not project from the bulb as it does in *Ocrepeira* (Fig. 123) or *Molinaranea* (Fig. 19). The paramedian apophysis (PM in Fig. 123) terminal apophysis (A), and subterminal apophysis (SA), not found in *Zygiella,* are present in *Ocrepeira* (Fig. 123) and *Molinaranea* (Fig. 19).

Natural History. This species is imported from Europe. In Chile, *Z. x-notata* is found on man-made structures, garden fences, houses. The upper half of the orb-web has a section that lacks sticky lines.

Records. ARGENTINA *Buenos Aires:* Buenos Aires, 25 Mar. 1912, 1♀ (J. Methes, MACN); Tres Arroyos, 38°23′S, 60°17′W, 15 Jan. 1943, 1♂ (Sorgentini, MLP); Estacíon Río Luján del Ferra Carril Mitre, 11 Jan. 1980, 2♀ (Zanetik, Goloboff, MACN). CHILE *Juan Fernandez Isl.:* Mas Afuera Quebrada Casa, 13–31 Mar. 1962, 1♀ (B. Malkin, AMNH). Common from Santiago south to Puerto Montt.

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A REVIEW OF THE GENUS *PSEDNOS* (PISCES, LIPARIDAE) WITH DESCRIPTION OF TEN NEW SPECIES FROM THE NORTH ATLANTIC AND SOUTHWESTERN INDIAN OCEAN

NATALIA CHERNOVA

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A REVIEW OF THE GENUS *PSEDNOS* (PISCES, LIPARIDAE) WITH DESCRIPTION OF TEN NEW SPECIES FROM THE NORTH ATLANTIC AND SOUTHWESTERN INDIAN OCEAN

NATALIA CHERNOVA[1]

ABSTRACT. A review of *Psednos* material examined since the study of Andriashev in 1992, who recognized two valid species, shows the existence of 12 species of which 10 are new: 8 in the North Atlantic and 2 in the southwestern Indian Ocean. The genus *Psednos* is rediagnosed and *P. micrurus* Barnard, 1927, and *P. christinae* Andriashev, 1992, are redescribed. The new species, *P. andriashevi* sp. nov. from off Ireland; *P. gelatinosus* sp. nov. and *P. micruroides* sp. nov., both from southeast of Greenland; *P. groenlandicus* sp. nov. from Davis Strait; *P. harteli* sp. nov.; *P. mirabilis* sp. nov., and *P. barnardi* sp. nov., all three from the western North Atlantic; and *P. sargassicus* sp. nov. from the northern Sargasso Sea, *P. steini* sp. nov. and *P. microps* sp. nov., both from the southwestern Indian Ocean, are described. A key to the identification of all known species is included. Based on numbers of vertebrae and sensory pores, two groups of *Psednos* can be recognized. Group 1 (vertebrae 41–43, coronal pore present, postorbital pore absent) contains *P. micrurus, P. mirabilis, P. micruroides, P. microps, P. sargassicus, P. steini,* and *Psednos* sp. 1. Group 2 (vertebrae 47, coronal pore absent, postorbital pore present) includes six species that occur in the North Atlantic: *P. christinae, P. andriashevi, P. barnadi, P. groenlandicus, P. harteli,* and *P. gelatinosus.*

INTRODUCTION

The then monotypic genus *Psednos* Barnard, 1927, was based on *P. micrurus* Barnard, 1927, which was described from two specimens caught off South Africa (Barnard, 1927a,b). The description and figure of the type specimens were poor and the holotype was thought to be lost for many years. *Psednos* was later included in the synonymy of the genus *Paraliparis* Collett by Stein (1979). Specimens of *Psednos* are extremely rare in museum collections. Stein (1979) described two specimens from the Indian Ocean, the first since Barnard, for which he gave a detailed description using the name *Paraliparis micrurus.* Andriashev (1992) found three more *Psednos* specimens from the eastern North Atlantic and studied the sensory system, cranium, and the anterior part of vertebral column and discovered some characters unique within the family Liparidae. The same characters were noted in the holotype of *P. micrurus* that by then had been found. As a result, the genus *Psednos* was validated and a new species *P. cristinae* Andriashev, 1992, was described (Andriashev, 1992, 1993a). The presence of two other undescribed species of *Psednos,* one from the eastern North Pacific (Andriashev, 1992; Stein, 1986a,b), and another from the eastern North Atlantic (Andriashev, 1992) have been noted. Thus, the discovery of a few additional specimens of *Psednos* in the collections of the Museum of Comparative Zoology, the United States National Museum, and the Zoological Museum, University of Copenhagen, is of great interest.

Study of the morphology of the new specimens shows that the material includes 10 undescribed species. Five of them (with vertebrae 41–43, coronal pore present, postorbital pore absent), described below as *P. micruroides* sp. nov., *P. mirabilis* sp. nov., *P. sargassicus* sp. nov., *P. steini* sp. nov., and *P. microps* sp. nov., are close to *P. micrurus* Barnard, 1927, whereas five others (with vertebrae 47,

[1] Zoological Institute, Russian Academy of Sciences, St. Petersburg, nchernova@hotmail.com Russia.

coronal pore absent, postorbital pore present) described below as *P. andriashevi* sp. nov., *P. harteli* sp. nov., *P. groenlandicus* sp. nov., *P. barnardi* sp. nov., and *P. gelatinosus* sp. nov., are closer to *P. cristinae* Andriashev, 1992. Comparison of the new material and the types of *P. micrurus* and *P. cristinae* allows a detailed analysis of the species and expanded diagnosis of the genus *Psednos*.

As noted above, *Psednos* material is very rare in museum collections. In this paper 12 species, 10 of which are previously unnamed, are reviewed based on 16 specimens, and one of the new species is entirely based on a previous literature account of a specimen that was incorrectly identified. Virtually no information is available on variation within a species. But the morphologic characters of the specimens are so different that no doubt exists that they are separate species.

MATERIALS AND METHODS

The methods used in this study follow Andriashev (1986, 1992) and Andriashev and Stein (1998). All proportions are in percent of standard length (SL) except those given in parentheses, which are in percent of head length (HL). Some proportions are explicitly specified as percent of the upper pectoral lobe (UPL). Counts were made from radiographs. Vertebral counts include the urostyle. The 1st caudal vertebra has a hemal spine aligned with the 1st anal ray. Subocular distance is measured on a line from the lower margin of the eye to the level of the posterior end of the mouth. Postocular distance is from the posterior margin of the eye to the end of the opercular flap. The diastema is the gap between the tooth bands of the premaxilla. The posterior tip of the lower jaw forms a distinct and prominent ventrally directed angle that is herein termed the retroarticular process (Fig. 1). The symphyseal knob is a short projection at the symphysis of the lower jaw. The trunk is the abdominal part of body from tip of snout to anal-fin origin. Color is described from specimens stored in alcohol.

The arrangement of cephalic pores and canals (Figs. 1–3) follows Andriashev (1992). The term "chin pores" is used for the symphyseal mandibular pores (anterior pores of the right and left preoperculomandibular canal).

Andriashev (1986) and Andriashev and Stein (1998) demonstrated the importance of the pectoral girdle in distinguishing among species and in explainng relationships in Liparidae. The number and shape of radials, whether notched or unnotched, their arrangement, and the presence or absence of interradial fenestrae are important. The shape of the coracoid or scapula and the associated lamellar struts or lateral ribs is also notable. The coracoid is usually shaped somewhat like a double-bladed axe and has a handlelike projection of variable length, and the length of the handle and the size of the lamellar plates are often species specific.

The following abbreviations for counts and measurements have been used.

Counts: a, anal-fin rays; C, caudal-fin rays; D, dorsal-fin rays; P, pectoral-fin rays; Radials, radials of pectoral girdle; V, vertebrae (abdominal + caudal).

Sensory Pores: cor, coronal; io, infraorbital; n, nasal; pm, preoperculo-mandibular; t, temporal.

Measurements: anusA, distance from center of anus to anal-fin origin; bd, maximum body depth (in *Psednos* at occiput); bdA, depth at anal-fin origin; eye, eye diameter horizontally; gsl, length of gill slit; HL, head length; HW, head width; io, interorbital width (between upper margins of eyes); LPL, greatest length of lower lobe of pectoral fin; mand-anus, length from mandibular symphysis to center of anus; notch, length of shortest notch ray of pectoral fin; postoc, postocular length; preA, preanal length; preD, predorsal length; snout, length from tip of snout to anterior margin of eye; SL, standard length; upj, upper jaw length; UPL, greatest length of upper lobe of pectoral fin.

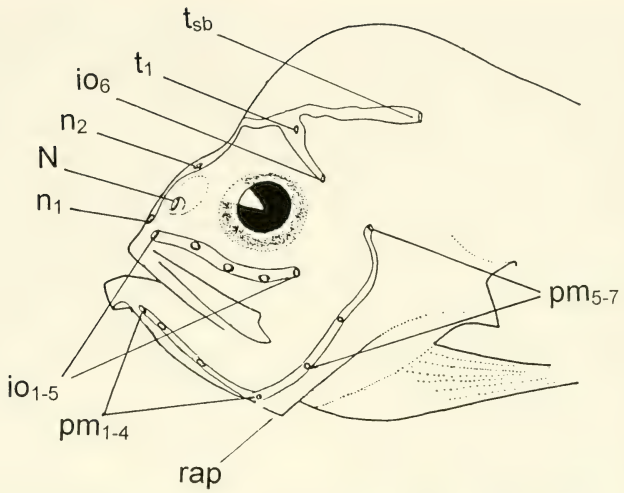

Figure 1. Diagram of cephalic sensory canals and pores (*Psednos christinae*) (from Andriashev, 1992). io_{1-5}, 1st to 5th infraorbital pores; io_6, separated upper infraorbital pore; N, nostril, n_1, lower nasal pore; n_2, upper nasal pore; pm_{1-4}, pm_{5-7}, 1st to 7th preoperculo-mandibular pores; t_1, 1st temporal pore; t_{sb}, suprabranchial temporal pore; rap, retroarticular process.

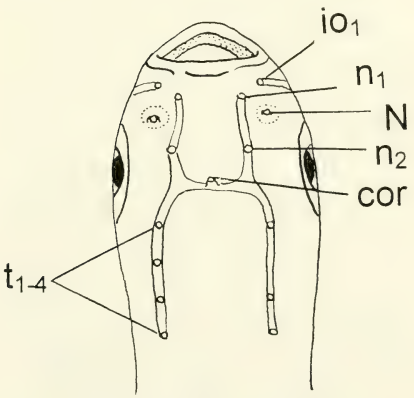

Figure 2. Sensory pores of *Psednos micruroides* sp. nov. Holotype. Head from above. Cor, coronal pore in the coronal commissura; t_{1-4}, 4 temporal pores; io_1, 1st infraorbital pore. Other abbreviations as in Figure 1.

Collection abbreviations follow Leviton et al. (1985) and Eschmeyer (1998) and Andriashev and Stein (1998) for ZISP (Zoological Institute of St. Petersburg, Russian Academy of Sciences).

All figures are drawn by the author.

SYSTEMATICS

Genus *Psednos* Barnard, 1927

Dwarf Snailfishes

Psednos Barnard, 1927a: 76; 1927b: 927 (type species *P. micrurus* Barnard, 1927, by monotypy).—Smith, 1953: 359 (sec. Barnard).—Stein, 1979: 5 (synonym of *Paraliparis* Collett).—Andriashev, 1992: 1 (valid; redescription).

Paraliparis (part): Stein, 1979: 6; 1986b: 493.—Andriashev, 1986: 14.

Diagnosis. Ventral disk absent. One pair of nostrils. No pseudobranchiae. Pleural ribs absent. Hypural plate single, unslit. Vertebrae 41–47, D 34–42, A 28–35. Body distinctly humpbacked at occiput. Anterior abdominal vertebrae and base of skull form an arch at almost a right angle.

Mouth oblique, superior or terminal. Teeth simple. Three radials in pectoral girdle, equally spaced, the lower radial largest. The upper nasal pore (n2) opens behind a vertical through or above nostril. Infraorbital sensory canal widely interrupted behind eye: infraorbital pores 6(5+1) or 5(5+0). Length to 53 mm SL.

Description. Body strongly humpbacked, its upper profile rises abruptly from short snout to high rounded occiput, then tapers more gently posteriorly (Fig. 4). Vertebral column in a S-shaped curve (Fig. 5). Base of skull (basioccipital in line with parasphenoid) almost forms a right angle with vertebral column; top of arch formed by 3 or 4 anterior vertebrae with neural spines that support the hump and are stronger and longer than others. Parapophyses of 2 or 3 posterior abdominal vertebrae obviously joined together forming gradually elongate hemal spines, the long hemal spine of 1st caudal vertebra fits to 1st anal ray. Upper pharyngeal teeth clearly seen on radiographs but lower ones not visible. Snout slanted and blunt, not projecting, rostral fold (a fold of skin forming part of ventral surface of snout immediately anterior to upper lip) not developed. Olfactory rosette visible through transparent skin. Suborbital bones usually extend anteriorly to form distinct projections above snout on either side of upper jaw. Retroarticular process at posterior tip of lower jaw distinct, with prominent ventrally directed angle (Fig. 1). Disastema present between anterior upper jaws. Operculum (Fig. 3C) very long, equal to or slightly exceeding ½ of head length. Lower jaw with or without symphyseal knob.

Morphology of sensory canals and pores of head unique within Liparidae, with nasal pores located high and infraorbital canal interrupted (Fig. 1). Because snout is short and slanted, 2 nasal pores of supraorbital canal located high, upper nasal pore n_2 opens behind vertical of nostril or above nostril. Coronal commissure with or without coronal pore (Fig. 2). Suprabranchial pore usually single, situated extremely high and forward, distance from it to dorsal end of gill slit 42–52% HL; 2 suprabranchial pores rarely present (Fig. 3B). Temporal pores usually 1+1, rarely 1+2, 0+1, or 3–4 pores in a row. Infraorbital canal widely interrupted behind eye, with 6(5+1) pores (Fig. 3B) or 5(5+0) (Figs. 3A, C); io6 pore, if present, opens at end of short canal directed down from beginning of temporal canal. Preoperculomandibular pores usually 6, rarely 7.

The 12 species of the genus *Psednos* reflect a bipolar (terminology of Berg, 1933) or antitropical distribution (Andriashev, 1991, 1993a; Hubbs, 1952) in pelagic or mesopelagic habitats of the temperate, subarctic and subtropical parts of the Northern and Southern hemispheres.

KEY TO SPECIES OF *PSEDNOS*

1a) Pectoral fin notched, with short intermedial notch rays, clearly bilobed. P 13–15 2

1b) Pectoral fin unnotched, without short notch rays, P 17. (Head small, about 22% SL, and much compressed, its width about ½ of head length; lower jaw teeth in double row; preanal 50% SL; coracoid with a handlelike projection; color grayish-brown. Off South Africa) ..... *P. microrus* Barnard

2a) Coronal pore present. V 41–43, D 34–38, A 28–31 3

2b) Coronal pore absent. V 47, D 38–42, A 33–35 8

3a) Gill slit completely above pectoral base; preanal not less than 40% SL (except *P. sargassicus* with preanal of 38.5% SL) 4

3b) Gill slit extending ventrally in front of 2–3 pectoral rays; preanal less than 40% SL. (Lower pectoral lobe longer than upper lobe; coracoid and scapula with handlelike projections. Eastern North Atlantic) ..... *Psednos* sp. 1 (*sensu* Andriashev, 1992)

4a) Eye greater than 20% HL 5

4b) Eye 13–15% HL 7

5a) Head large, greater than 28% SL; color pale (western North Atlantic) 6

5b) Head about 25% SL. Color tan (southwestern Indian Ocean) ..... *P. steini* sp. nov.

6a) Temporal pores 3–4; gill slit equal to eye; P 13(7+1+5) with 1 ray in pectoral notch (southeast of Greenland) ..... *P. microroides* sp. nov.

6b) Temporal pores 1+1; gill slit 2 times eye diameter; P 13(8+0+5) without notch

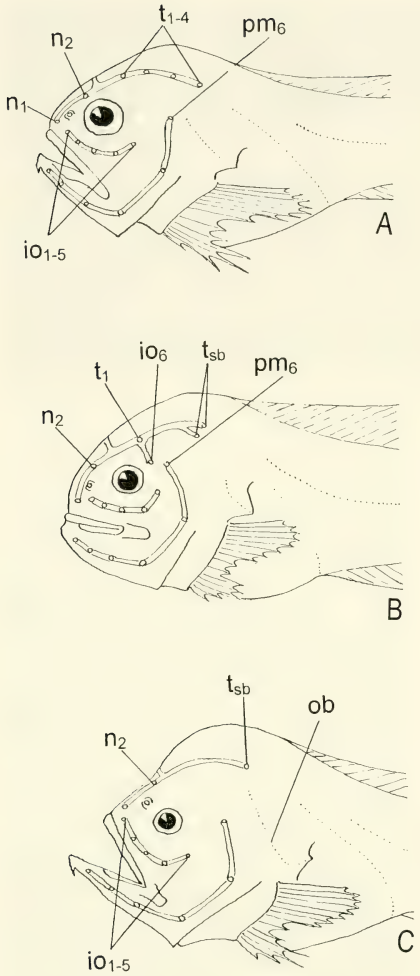

Figure 3. Sensory pores in three new species of *Psednos* in lateral view. (A) *P. micruroides* sp. nov., temporal pores 4, t_{1-4}; io_6 absent, infraorbital pores 5(5+0). (B) *P. gelatinosus* sp. nov.; temporal pores t 1+2 including 2 suprabranchial pores, t_{sb}; infraorbital pores io 6(5+1), io_6 present; preoperculo-mandibular pores 6, pm_6 close to io_6 and level with it. (C) *P. microps* sp. nov.; 1st temporal pore absent, t 0+1; io 5(5+0); ob, opercular bone. Other abbreviations as in Figures 2, 3A,B.

ray (off New England) ..... *P. mirabilis* sp. nov.

7a) First temporal pore absent, t 0+1; head 29.4% SL (southwestern Indian Ocean) ..... *P. microps* sp. nov.

7b) Temporal pores 1+1; head 25% SL (northern Sargasso Sea) ..... *P. sargassicus* sp. nov.

8a) Preoperculo-mandibular pores 7 (eastern North Atlantic) 9

8b) Preoperculo-mandibular pores 6 (western North Atlantic) 10

9a) Opercular flap small and triangular, its tip clearly below the level of eye; gill slit small, 20.4–21.5% HL or less than eye diameter (0.8–0.9); P 15(8+1+6) with 1 notch ray; head 24–25% SL; eye 24–26% HL ..... *P. christinae* Andriashev

9b) Opercular flap long and winglike, its tip level with pupil; gill slit large, ca. 28% HL or 1.3 times eye diameter; P 15(8+2+5) with 2 notch rays; head 27% SL; eye 21% HL ..... *P. andriashevi* sp. nov.

10a) One suprabranchial pore; pm_6 pore below level of io_6 pore; caudal part of body entirely pale or its end only slightly pigmented; dorsal and anal fins overlap ⅓ of caudal fin 11

10b) Two suprabranchial pores; pm_6 pore level with io_6 pore; margins of D and A blackish only at their middle portion; dorsal and anal fins overlap ⅔ of caudal fin. (Eye 17.4% HL; body very gelatinous. Off Greenland) ..... *P. gelatinosus* sp. nov.

11a) Gill slit about equal to eye diameter; eye 20–21% HL 12

11b) Gill slit 1.7 times eye diameter; eye smaller, 18% HL ..... *P. barnardi* sp. nov.

12a) Lower pectoral lobe wide and thick, hand-like (Fig. 6A), pectoral notch with only 1 ray; gill slit distinctly oblique; mouth cleft reaching to below pupil; upper jaw 13.5% SL; caudal part of body and vertebrae unpigmented ..... *P. harteli* sp. nov.

12b) Lower pectoral lobe with thin and elongate rays (Fig. 6B), pectoral notch with 2 rays; gill slit almost vertical; mouth cleft reaching to below anterior margin of eye; upper jaw 10.6–12.6% SL; slight dark pigmentation present on caudal part of body and along posterior vertebrae ..... *P. groenlandicus* sp. nov.

Psednos andriashevi new species

Andriashev's Dwarf Snailfish (Fig. 7A)

Psednos christinae (non Andriashev, 1992): Andriashev, 1992: 10, figs. 3b, 7; 1993a: 9, figs. 2A, 6 (ex parte: only specimen ISH 574-1986, SL 53 mm).

Material. Holotype. ISH 574-1986, adult male 53 mm SL. R/V *Walter Herwig*, Sta. 419/86. West of

Ireland, 54°21′N, 17°59′W, 4 Jul. 1986, depth 800 m. Midwater trawl. Coll. A. Post. This specimen was designated as 1 of 2 paratypes of *P. christinae* by Andriashev (1992: 10, fig. 3b—radiograph, fig. 7—pectoral girdle).

Diagnosis. A *Psednos* from the North Atlantic with V 47, D 42, coronal pore absent, 7 preoperculo-mandibular pores. Head large (27% SL) and very compressed (40% HL); gill slit large (28% HL or 1.3 eye diameter), opercular flap long, winglike, reaching behind midpectoral length and level with pupil. Pectoral fin short (45% HL), with 2 notch rays.

Description. Dorsal outline sloping gently from high occiput caudally. Ends of first 3 neural spines clearly prominent above dorsal contour of body. Maximum depth at occiput 4.1 in SL or 1.7 times depth at anal-fin origin; trunk short, preanal 35% SL. Dorsal and anal fins low. Caudal fin rays missing. Anus on vertical through ⅗ of postocular distance and just in front of ventral end of gill slit. Pyloric caeca 6.

Head large, 3.7 times in SL, very compressed (40% HL or 2.2 times in head depth). Depth at occiput less than head length (90% HL). Anterior profile of head slopes straight down to tip of short snout with a slight concavity in front of eye. Snout length equal to eye diameter. Nostril level with eye center. Eye not large (4.8 in HL), pupil ca. ¾ of eye diameter. Interorbital 1.6 eye diameter. Suborbital distance about equal to eye diameter. Mouth oblique, terminal, forming an angle of about 45° to the horizontal, symphysis of upper jaw level with lower margin of eye. Mouth cleft reaching vertical to anterior margin of pupil, maxillary to vertical of posterior margin of pupil. Teeth sharp, in oblique rows, 5 teeth per row near symphysis of upper and lower jaws. Diastema of upper jaw narrow. Lower jaw slightly projecting. Chin not deep, lower jaw not massive. Symphyseal knob present. Prominent tip of lower jaw (retroarticular process) is on vertical with posterior margin of eye.

Gill slit entirely above pectoral fin base, long (28% HL and 1.3 eye diameter) and located high: dorsal end level with upper margin of pupil, ventral end level with ⅔ of subocular distance. Gill slit oblique, its dorsal end distinctly behind the vertical of its ventral end. Opercular flap long, its shape unique in *Psednos,* with a prominent, winglike end reaching posteriorly to behind middle of pectoral fin. Operculum directed posterodorsally, its end level with upper half of pupil. Gill rakers 9, with small prickles on top.

Pectoral fin 15(8+2+5) with 2 notch rays. Upper pectoral lobe short, only 45% HL, reaching almost to anal-fin origin. Uppermost pectoral ray level with lower third of subocular space. Lowermost pectoral ray based approximately on a vertical through middle of postocular distance. Lower pectoral lobe almost reaching to vertical through end of upper lobe. Radials 3, rounded, lowermost largest. Fenestrae in cartilaginous basal lamina absent (see Andriashev, 1992, fig. 7). Scapula small, with short upward-directed handlelike projection. Coracoid large, half-moon in shape, without handlelike projection.

Vertebrae 47(10+37), parapophyses of 3 posterior abdominal vertebrae forming short hemal spines. Interneural of 1st dorsal ray fits between 4th and 5th neural spines.

Sensory System. Coronal pore absent. Nasal pores 2, upper as small as nostril and level with upper margin of pupil. Temporal pores 1+1, infraorbital 6(5+1), preoperculo-mandibular 7. Distance between chin pores (pm_1–pm_1) slightly larger than distances between pm_1 and pm_2.

Measurements and Counts: HL 27.2, HW 10.9 (40.3), bd 24.5 (90), bdA 14.7 (54), preD 28.3 preA 34.9, mand-anus 19.8, anusA 15.3, UPL 12.3 (45), LPL 13.2 (107% UPL), snout 5.7 (20.8), eye 5.7 (20.8), postoc 15.1 (56), io 9.1 (33.3), gsl 7.5 (27.8), upj 11.9 (44). V 47(10+37), D 42, A 36, P 15(8+2+5), C 6. Radials 3, rounded.

Color. Skin uniformly pale, caudal part

Figure 4. *Psednos barnardi* sp. nov. Male, 34-mm standard length. Holotype (right side). Photograph by K. E. Hartel.

of body without pigmentation. Head and belly appear dark because of the color of peritoneum, mouth, and gill cavity. Peritoneum brownish-black, stomach lighter but also blackish, pyloric ceca light brownish-black, intestine slightly pigmented. Gill arches brownish. Mouth light brownish-gray. Gill cavity dark brown. Ventral surface of head unpigmented.

Distribution. Known only from the holotype taken in the eastern North Atlantic, west of Ireland, in midwater at a depth of 800 m.

Etymology. This species is named for the well-known Russian ichthyologist Anatole P. Andriashev who, in particular, made the definitive morphologic study of the genus *Psednos*.

Taxonomic Notes. This specimen was designated as a paratype of *P. christinae* by Andriashev (1992, 1993a), but during the preparation of his work the specimen was on loan in the USA and was not studied in detail, with the exception of its radiograph and pectoral girdle (Andriashev, 1992: 15).

Comparative Notes. Psednos andriashevi belongs to a species group with 47 vertebrae, no coronal pore, 6(5+1) io pores, and 7 preoperculo-mandibular pores. Its long winglike opercular flap reaching behind the middle of pectoral length is unique among *Psednos*. It is also distinguished by the following: the head is large (27% SL) and compressed (its width 40% HL), long gill slit (28% HL or 1.3 eye diameter) and located high (end of operculum level with pupil), the pectoral fin short (45% HL) and has 2 notch rays. It is most similar to the sympatric *P. christinae*, which differs in having a small triangular opercular flap, a smaller gill slit (20.4% HL or 0.8–0.9 eye diameter), a lower opercular end that is clearly below eye, a smaller (24% SL) and wider head (50% HL), a longer pectoral fin (66% HL), and only 1 notch ray. Differs from *Psednos* sp. 1 (*sensu* Andriashev, 1992) from the eastern North Atlantic by vertebral number (47 vs 43) and absence of coronal pore (vs presence).

Psednos barnardi new species

Blackchin Dwarf Snailfish (Figs. 4, 7B)

Material. Holotype. MCZ 155422, subadult male 34 mm SL. R/V *Delaware II*, Cr. 99-02, Sta. 14, WN Atlantic, 39°49′N, 70°39′W, 04 Feb. 1999, over bottom at 1042–1368 m. Paratype. MCZ 63036, juv. 15 mm SL. R/V *Oceanus*, Cr. 125, 39°11′24″N, 70°59′6″W, 22 Aug. 1982. Multiple opening closing net MOC 20-054,1, depth 1001–750 m.

Diagnosis. A *Psednos* from the North

Atlantic with V 47, D 39–41, no coronal pore, 6 preoperculo-mandibular pores, a small eye (18% HL), gill slit 1.6 eye diameter, and a short mouth (its cleft reaching to below anterior margin of eye). Caudal part of body unpigmented, skin on chin and lower jaw black.

Description. Maximum depth at occiput 3.5 in SL and 1.9 times greater than depth above anal-fin origin. Trunk rather long, preanal distance 38% SL. Dorsal and anal fins low and long, overlaping 40% of caudal fin. Anus on vertical at about middle of postocular distance. Skin semitransparent. Subcutaneous gelatinous tissue weakly developed.

Head not large, 3.8 in SL, but compressed (width 56% HL) or 2 times in depth. Depth at occiput greater than HL (110%). Anterodorsal profile abruptly rounded to tip of snout. Snout 1.9 times larger than eye. Nostril small, porelike, level with eye center. Eye small, 6 times in HL, pupil ca. ¾ of eye diameter. Interorbital 3.3 eye diameter. Subocular distance 1.6 eye diameter. Mouth superior, oblique, forming an angle of about 35° to the horizontal. Symphysis of upper jaw in line with upper ⅕ of subocular distance. Mouth short, its cleft reaching at vertical from anterior margin of eye, upper jaw reaching to vertical from posterior margin of eye. Lower jaw projecting. Lips thin, lower lip with lateral lobe. Symphyseal knob present. Prominent tip of lower jaw (retroarticular process) just behind vertical at posterior margin of eye. Teeth sharp and large in both jaws, 4 and 5 in 1st full row near symphysis of upper and lower jaw. Upper jaw with narrow diastema.

Gill slit slightly oblique, 1.6 larger than eye, completely above pectoral base and placed high; its dorsal end level with lower margin of pupil, ventral end almost level with end of mouth cleft. Opercular flap triangular. Operculum directed backward, its end level with middle of subocular space.

Pectoral fin P 14(8+1+5), with 1 notch ray that is clearly separate from other rays. Uppermost pectoral ray level with posterior end of oblique mouth, lowermost pectoral ray based on vertical of ca. ⅕ of postocular space. Upper lobe almost reaching to anal-fin origin. Lower lobe rays thin, elongate.

Vertebrae 47(10+37), parapophysis of 10th vertebrae form a short hemal spine, not reaching 1st interhemal. Interneural of 1st dorsal ray fits between neural spines of 5th and 6th vertebrae.

Sensory System. Coronal pore absent. Nasal pores 2, n_2 pore level with upper margin of eye. Infraorbital 6(5+1), io_6 pore placed behind upper margin of eye. Temporal 1+1, 1st temporal pore (t_1) slightly larger than io_6; suprabranchial pore located at a distance of 44% HL from dorsal end of gill slit. Preoperculo-mandibular 6, chin pores (pm_1–pm_1) spaced at a distance equal to pm_1–pm_2.

Measurements and Counts. HL 26.4, HW 14.7 (56), bd 28.8 (109), bdA 15.3 (58), preD 31.5, preA 38.2, mand-anus 20.3, anusA 22.1, UPL 17.9 (68), LPL 11.2 (63% UPL), snout 8.2 (31.1), eye 4.7 (17.8), postoc 17.6 (67), io 15.3 (58), gsl 7.4 (27.8), upj 13.5 (51.1). V 47(10+37), D 39–41, A 33–35, P 14(8+1+5), C 6. Radials unknown.

In the 15-mm-SL juvenile, the number and location of sensory pores and relative position of nostril, eye, gill slit, mouth, and pectoral fin are the same as the holotype. Proportions of head and body are also similar with the exception of head, which is larger (31.3 vs 26.4% SL), and the eye, which is much smaller (14.6 vs 17.8% HL). D ca. 41, A 35, C 6.

Color. Skin light, unpigmented; caudal part of body milky-pale. Head and belly appear bluish-black because of color of peritoneum, mouth, and gill cavity, which can be clearly seen externally. Margin of opercular flap and gill slit area black. Skin on chin, lower jaw, mouth, and lips black; lateral lobe of lower lip whitish. Pectoral fin light but its lowermost ray blackish. Anal area blackish.

Etymology. This species is named after Keppel Harcourt Barnard, the South Af-

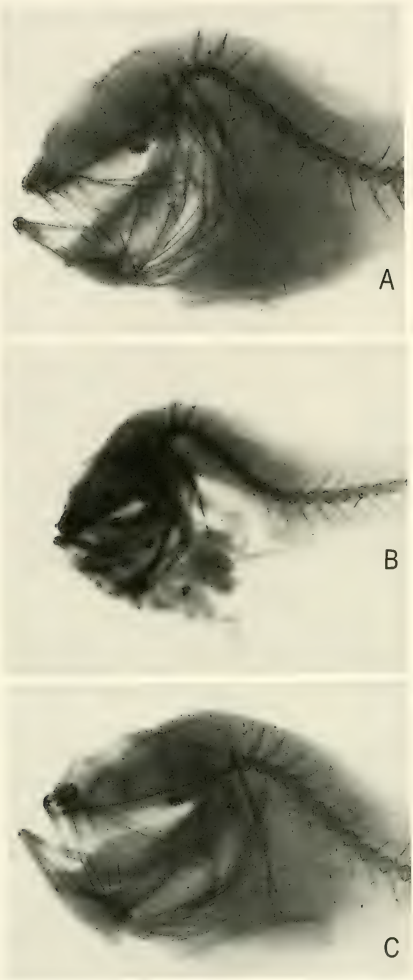

Figure 5. Radiographs of *Psednos*. (A) *P. harteli* sp. nov., holotype. (B) *P. groenlandicus* sp. nov., holotype. (C) *P. micruroides* sp. nov., holotype.

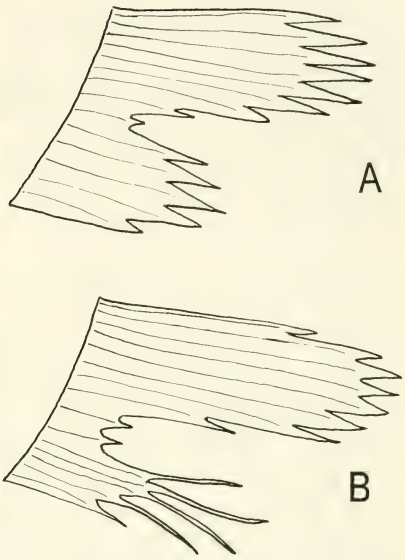

Figure 6. Right pectoral fins of two *Psednos*. (A) *P. harteli* sp. nov., holotype. (B) *P. groenlandicus* sp. nov., holotype.

rican ichthyologist, who first described the genus *Psednos*.

Distribution. This species is known only from the western North Atlantic near the southeast slope off New England (about 40°N), at a depth of 1042–1368 m for the adult and between 750 and 1001 m for the juvenile.

Comparative Notes. Psednos barnadi belongs to a group of *Psednos* with 47 vertebrae, no coronal pore, 6(5+1) io pores, and 6 preoperculo-mandibular pores. It is distinguished by a small eye (18% HL), a gill slit that is 1.6 eye diameters, a short mouth cleft, an unpigmented caudal part of body, and black skin on chin. It is most similar to *P. groenlandicus* but differs from it by a smaller eye (18 vs 20–23% HL), a larger gill slit (1.6 vs about equal to eye) that is more highly located (its dorsal end level with eye center vs below the level of eye), a shorter mouth cleft reaching to below anterior margin of eye (vs eye center), a smaller subocular space (1.7 times eye vs about equal to eye), pectoral fins with 1 notch ray (vs 2 notch rays), milky-pale caudal part of body (vs with black pigmenta-

tion), and the skin on chin and lower jaw black (vs strictly unpigmented). The head and belly look much blacker than in *P. groenlandicus*, the caudal part looks more low and elegant, and the subcutaneous gelatinous tissue is less developed.

Psednos christinae Andriashev, 1992

European Dwarf Snailfish (Figs. 1, 7C)

Psednos christinae Andriashev, 1992: 10, figs. 4, 5a, 6; 1993a: 9, figs. 3–5 (ex parte: the holotype ISH 741-82 and 1 of 2 paratypes, ZISP 49982).

Psednos christinae (non Andriashev, 1992): Andriashev, 1992: 10, figs. 3b, 7; 1993a: 9, figs. 2A, 6 (ex parte: 1 of 2 paratypes of *P. christinae*, ISH 574-86, 53 mm SL = holotype of *P. andriashevi* sp. nov., see above).—Kido et Yabe in Okamura et al., 1995: 185, fig. 128 (1 sp. SL 58 mm, East Greenland = undescribed species).

Material. Holotype. ISH 741-1982, adult male 45.5 mm. R/V *Walter Herwig*, Sta. 392/82. East slope of the northernmost part of the Mid-Atlantic Ridge, 49°48′N, 25°55′W, 16 Jun. 1982. Depth 1000 m. Coll. C. Karrer. Paratype. ZISP 49982, adult male 45 mm. R/V *Walter Herwig*, Sta. 321/83. West of Scotland, 56°22′N, 11°55′W, 18 May 1983. Depth 1500 m. Coll. N. Merrett.

Diagnosis. A North Atlantic *Psednos* with V 47, D 41, coronal pore absent, 7 preoperculo-mandibular pores, a short head (24–25% SL), small gill slit (20.4–21.5% HL or 0.8–0.9 eye diameter) that is low (end of operculum below level of eye), opercular flap small, triangular; pectoral fin long (66% HL) with 1 notch ray and uppermost ray level with posterior end of mouth cleft.

Description. Maximum depth (at occiput) 3.8 in SL, about 2 times greater than depth at anal-fin origin. Trunk not long, preanal 34% SL. Dorsal and anal fins low. Anus on vertical with ½ of postocular distance.

Head 4.0 times in SL, compressed, its width about 53% HL or 2 times in head depth. Depth at occiput greater than head length, 106 (116)% HL. Anterodorsal profile straight, sloping to tip of snout, but slightly concave above eye. Snout 1.1 times eye. Nostril small, level with eye center. Eye 4.2 in HL, pupil ⅔ of eye diameter. Interorbital 1.5 times eye. Suborbital distance about equal to eye. Mouth superior, oblique, forming an angle of about 40–45° to horizontal. Symphysis of upper jaw level with lower margin of eye. Mouth cleft reaching to anterior ½ of pupil, end of upper jaw to posterior margin of eye. Lower jaw projecting. Symphyseal knob large. Chin low, lower jaw not massive. Prominent tip of lower jaw (retroarticular process) on vertical with posterior margin of pupil, angled at about 90°. Teeth sharp, 5–7 and 6–7 teeth in each row near symphysis of upper and lower jaw. Diastema of upper jaw narrow.

Gill slit small (0.8–0.9 of eye diameter), almost vertical, entirely above pectoral base; located low, its dorsal end level with lower margin of eye, ventral end level with posterior end of oblique mouth. Opercular flap short, triangular, reaching posteriorly to point not more than a vertical of 1/5 of pectoral fin length. Operculum directed ventroposteriorly; its end level with lower ⅓ of subocular distance. Gill rakers 11, with tiny, dorsal prickles.

Pectoral fin located low, its uppermost ray level with posterior end of oblique maxilla. Pectoral notch with 1 ray, P 15(8+1+6), in paratype 15(9+1+5). Upper pectoral lobe long, 66% HL, almost reaching anal-fin origin. Lowermost ray inserted in vertical at third of postocular space. Rays of lower lobe thin and elongate, their length about 90% of upper lobe length. Pectoral girdle radials 3, rounded, equally spaced. Lowermost radial about twice as large as upper. Fenestrae in basal cartilaginous lamina absent. Scapula with short, stout, anteriorly directed handlelike process. Coracoid large, half-moon shaped (Fig. 8A).

Vertebrae 47(47): abdominal 10(10), caudal 37(37). Interneural of 1st dorsal ray fits between 4th and 5th vertebrae.

Sensory System. Coronal pore absent. Nasal pores 2, n_2 pore level with upper margin of eye. Infraorbital 6(5+1), temporal 1+1, preoperculo-mandibular 7.

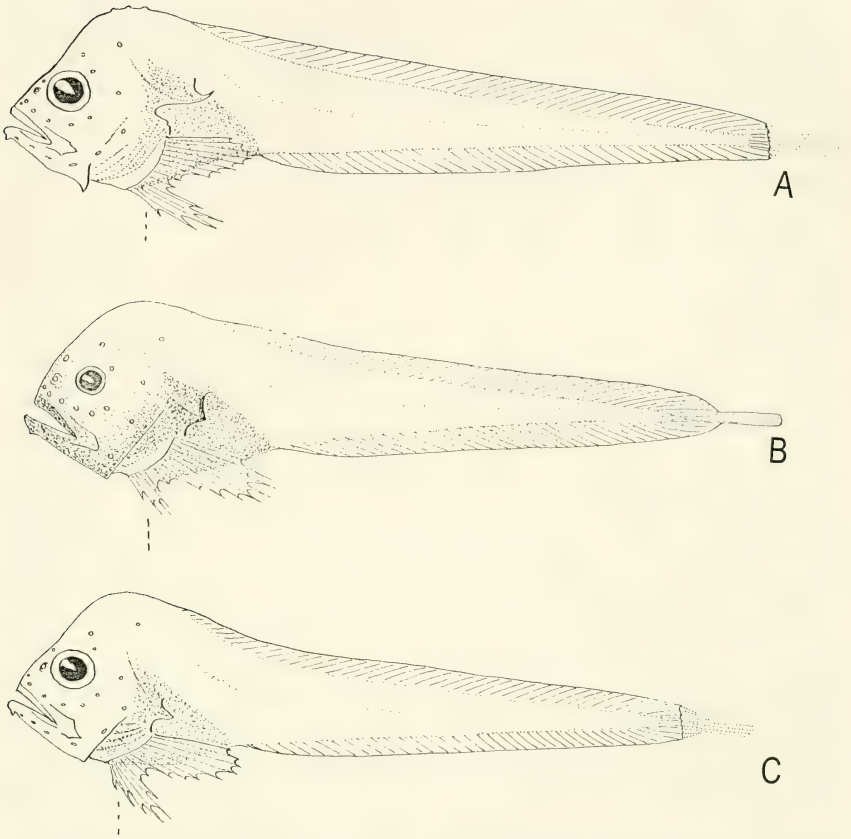

Figure 7. Three species of *Psednos*. (A) *P. andriashevi* sp. nov. Male, 53 mm. Holotype ISH 574-1986. West of Ireland, 800 m. (B) *P. barnardi* sp. nov. Male, 34-mm standard length (SL). Holotype MCZ 155422. Western North Atlantic, 1042–1368 m. (C) *P. christinae* Andriashev, 1992. Male, 45.5-mm SL. Holotype ISH 741-1982. Northernmost part of the Mid-Atlantic Ridge, eastern slope, 1000 m.

Chin pores (pm_1–pm_1) spaced at a distance equal to pm_1–pm_2.

Measurements and Counts. In percentage of SL (data for 45-mm-SL paratype in parentheses): HL 24.9 (23.8), HW 13.2 (12.7), bd 26.4 (27.8), bdA 14.9(—), preD 27.0 (27.8), preA 34.1 (34.9), mand-anus 19.8 (18.9), anusA 18.3 (18.9), UPL 16.5 (16.8), notch ray 5.5 (5.7), LPL 13.2 (14.2), eye 5.9 (6.2), snout 6.8 (—), io 8.8 (9.3), postoc 14.2 (—), upj 10.6 (11.1), gsl 5.1 (5.1), as percentage of HL: HW 53.0 (53.4), bd 106 (116), bdA 60, UPL 66.3 (—), eye 26.2 (23.9), snout 26.6 (25.3), io 35.4 (39.3), postoc 57 (—), upj 42.5 (46.8), gsl 20.4 (21.5). V 47(10+37), D 41, A 35, P 15(8–9+1+5–6), C 6. Radials 3, rounded.

Color. Skin uniformly pale but head and belly look dark because dark color of mouth and peritoneum, which can be seen externally. Mouth black, gill arches and rakers dark gray, gill cavity and peritoneum blackish-brown. Skin on ventral surface of head unpigmented. Stomach brownish-black. Pyloryc ceca brownish, melanophores few but arranged more densely near base of appendages. Intestine pale.

Distribution. Holotype caught on the east slope of northernmost part of the Mid-Atlantic Ridge at 1000 m; paratype taken in midwater, west of Ireland at a depth of 1500 m, over a great depth.

Comparative Notes. Psednos christinae belongs to a species group with 47 vertebrae, no coronal pore, 6(5+1) io pores, and 7 preoperculo-mandibular pores. It is distinguished by an unusually short gill slit (20.4–21.5% HL or 0.8–0.9 eye diameter) that is located low (its dorsal end level with lower margin of eye), a small triangular opercular flap with its tip below the level of eye, and a long pectoral (66% HL) with 1 notch ray that is placed low. It is most similar to the sympatric *P. andriashevi* (see comparative notes for that species).

Psednos christinae differs from *P. micrurus* because it has more vertebrae (47 vs 43) and fin rays (D 41 vs 37, A 35 vs 30), a shorter preanal distance (34 vs ca. 50% SL), a clearly notched pectoral fin (vs obviously unnotched), 5–7 teeth in a row near symphysis of lower jaw (vs in double row), and by the color of the gill cavity and peritoneum (black vs dark brown). In *P. christinae*, the coracoid is half-moon in shape (with a short stout handle in *P. micrurus*).

Psednos gelatinosus new species

Gelatinous Dwarf Snailfish (Figs. 3B, 9A)

Material. Holotype. MCZ 64537, juvenile male, 30 mm SL, 34.5 mm TL. R/V *Endeavor*, Cr. 133, SE of Greenland, 63°05′54″N, 39°39′54″W, 14 Aug. 1985, EN 133-19, 1330 mwo, depth 0–650 m. Coll. David Backus.

Diagnosis. A North Atlantic *Psednos* with D 38, A 35, no coronal pore, 6 preoperculo-mandibular and 2 suprabranchial pores; head large (29% SL), eye small (17.4% HL), mouth slightly oblique and short (its cleft reaching to below anterior margin of eye); dorsal and anal fins overlap ⅔ of caudal fin; body greatly gelatinous; color pale with dark margins near middle of dorsal and anal fins.

Description. Body moderately humpbacked, depth at occiput 3.7 times in SL and 1.5 times depth at anal-fin origin. Trunk rather large, preanal 38% SL. Dorsal and anal fins deep and overlap ⅔ of caudal fin. Anus on vertical at ¾ of postocular distance. Pyloric ceca not studied because belly not dissected. Skin semitransparent. Subcutaneous gelatinous tissue well developed, so much so that body seems to be inserted in gelatinous sack.

Head large, 3.5 times in SL, and wide (about 70% HL). Depth at occiput about equal to head (105% HL). Anterodorsal profile rounded to tip of snout. Nostril small, level with lower margin of eye. Eye round, small, 5.7 times in HL. Pupil about ¾ of eye diameter. Mouth terminal, only slightly oblique, forming an angle 15–20° to horizontal. Symphysis of upper jaw below level of lower margin of eye. Mouth cleft reaching to below anterior margin of eye, maxilla reaching to its posterior margin. Lower jaw slightly projecting. Symphyseal knob present. Lips thins, lower lip with a lateral lobe. Chin deep, lower jaw massive. Retroarticular process on a vertical at ⅕ of postocular distance. Teeth sharp, in numerous oblique rows, containing 5–6 teeth in both lower and upper jaws near symphysis.

Gill slit slightly oblique and 1.5 times larger than eye diameter, completely above pectoral base; its dorsal end level with eye center. Opercular flap triangular. End of operculum posteroventrally directed and level with middle of suborbital distance.

Pectoral fin 15(8+1+6), upper lobe about 64% HL, not reaching anal-fin origin. One notch ray, its length about 38% of upper lobe. Uppermost pectoral ray lev-

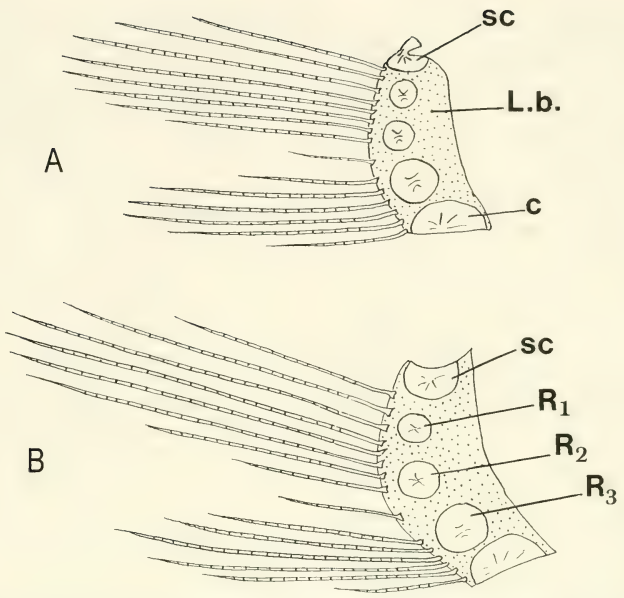

Figure 8. Right pectoral girdle and fin (right from outside) of two *Psednos*. (A) *P. christinae* Andriashev, 1992, holotype. (B) *P. groenlandicus* sp. nov., holotype. c, coracoid; L.b., basal cartilaginous lamina; R_1, R_2, and R_3, radials; sc, scapula.

el with symphysis of upper jaw. Lowermost pectoral ray inserted an eye diameter behind prominent posterior tip (retroarticular process) of lower jaw and on a vertical to about ⅔ of postocular distance.

Radiograph does not show vertebrae or fin rays, possibly because of lack of ossification as species of *Psednos* of same size show distinct vertebrae and fin rays.

Sensory System (Fig. 3B). No coronal pore. Two nasal pores, about twice as large as nostril diameter, n_2 pore level with upper margin of eye and distinctly above nostril. Infraorbital 6(5+1); io_{1-5} pores situated in semicircle below eye, gradually increasing in diameter from 1st to 4th, with 5th smaller than 4th and 6th situated just behind posterodorsal margin of eye. Temporal pores 1+2, t_1 round, about 1.5 times larger than io_6; suprabranchial pores 2, each at end of its own tube, situated one above another, lower pore at 52% HL from dorsal end of gill slit. Preoperculomandibular 6, position of the pm_6 unique to this species of *Psednos*: situated high, level with io_6 pore, and very close to latter. Chin pores (pm_1–pm_1) spaced at a distance equal to pm_1–pm_2.

Measurements and Counts. HL 28.6, HW 20.7 (72.1), bd 30.0 (105), bdA 20.3 (70), preD 34.0, preA 38.3, mand-anus 23.3, anusA 23.3, UPL 18.3 (64.0), notch 7.0, LPL 10.7 (60% UPL), eye 5.0 (17.4), snout 10.0 (34.9), io 17.3 (60.5), postoc 17.3 (60.0), upj 16.0 (55.8), gsl 8.0 (27.9). V unknown, D ca. 38, A ca. 35, P 15(8+1+6), C 6.

Color. Skin uniformly light, caudal part of body unpigmented. Margins of dorsal and anal fins black at midlength of fins. Margin of opercular flap also black. Head and belly appear dark because of dark

mouth and peritoneum that is visible externally. Skin on head light, only the lips are slightly pigmented but not black. Mouth and gill cavity brownish-black. Peritoneum dark.

Distribution. Known only from one specimen collected off southeast Greenland, in midwater at a depth of 0–650 m.

Etymology. The name "gelatinosus" reflects the great development of subcutaneous gelatinous tissue in this species.

Comparative Notes. Psednos gelatinosus belongs to a species group with about 47 vertebrae, 38–42 D rays, no coronal pore, 6(5+1) io pores, and 6 preoperculo-mandibular pores. It is unique because of presence of 2 suprabranchial pores; all other known species of *Psednos* have only 1 suprabranchial pore. Position of pm_6 pore (close to io_6 and level with it) is also very unusual as is very gelatinous body and black margins at midlength of dorsal and anal fins. Mouth only slightly oblique with short cleft only reaching to below anterior margin of eye. Dorsal and anal fins are deep and overlap ⅔ of the length of the caudal fin. Most similar to *P. harteli* sp. nov. and *P. groenlandicus* sp. nov. but differs by above characters.

Psednos groenlandicus new species

Greenland Dwarf Snailfish (Figs. 5B, 6B, 8B, 9B)

Material. Holotype. ZMUC P 82660, adult male, 39.5 mm SL, 46 mm TL. R/V *Paamiut*, Trawl 12. Davis Strait, 64°30′N, 56°17′W, 27 Sep. 1997, depth 930 m, bottom temperature 3.5°C. Coll. P. R. Møller. Pectoral girdle preparation No 744. Paratype. ZMUC P 82763, adult male, 53 mm SL, 62 mm TL. R/V *Shinkai Maru*, Trawl 3, 63°26.7N, 53°54.7W, 5 Aug. 1991, depth 1055 m, bottom trawl. Coll. P. R. Møller. Additional material: ZMUC P 82519, dry specimen ca. 45 mm SL. R/V *Shinkai Maru*, trawl 64, 65°09′N, 56°07′W, 23 Aug. 1992. Coll. P. R. Møller.

Diagnosis. A North Atlantic *Psednos* with V 47, D 41, coronal pore absent, 6 preoperculo-mandibular pores, 1 suprabranchial pore, short mouth cleft (reaching to below anterior margin of eye), upper jaw short 10.6–12.6% SL; vertical gill slit about equal to eye diameter and placed low, pectoral notch with usually 2 rays, and with slight blackish pigmentation at end of caudal part of body and along vertebrae.

Description. Depth at occiput 4 times in SL and 1.7 (1.8) times depth at anal-fin origin. Trunk not long, preanal 38 (36)% SL. Dorsal and anal fins not deep and overlap ⅓ of caudal fin. Anus on vertical near middle of postocular space. Pyloric ceca 5, short and paddlelike with roundish tips (not fingerlike with sharp tips as in *P. christinae*). Skin semitransparent, subcutaneous gelatinous tissue comparatively well developed.

Head 4 (4.3) times in SL, quite compressed, its width 60 (51)% HL and 2.3 times in head depth. Head deep at occiput, depth greater than head length (115% HL). Anterodorsal profile abruptly rounded to tip of snout. Snout 1.4 times larger than eye. Nostril small and porelike, level with lower ½ of eye. Eye round, 4.9 (4.4) times in HL, pupil about ½ of eye diameter. Mouth cleft terminal, oblique, forming an angle of about 30 (35)° to horizontal. Symphysis of upper jaw slightly below level of lower margin of eye. Mouth cleft reaching posteriorly to a vertical with anterior margin of eye, maxillary almost to posterior margin of eye. Lips thin, lower lip with narrow lateral lobe. Lower jaw slightly projecting; symphyseal knob, if present, very small and hardly distinguished on specimen or on radiographs and not developed as in *P. micrurus, P. christinae*, and *Psednos* sp. 1 (Andriashev, 1992, fig. 3). Prominent tip of lower jaw (retroarticular process) on vertical with posterior end of eye (of pupil in paratype). Teeth sharp, closely set in numerous oblique rows of 6–7 (5–6) teeth in lower and upper jaws near symphysis. Upper jaw diastema narrow.

Gill slit almost vertical and not larger than eye diameter, completely above pectoral base and located low, dorsal end of gill slit about level with middle of subocular space, its ventral end level with end of oblique mouth. Opercular flap triangu-

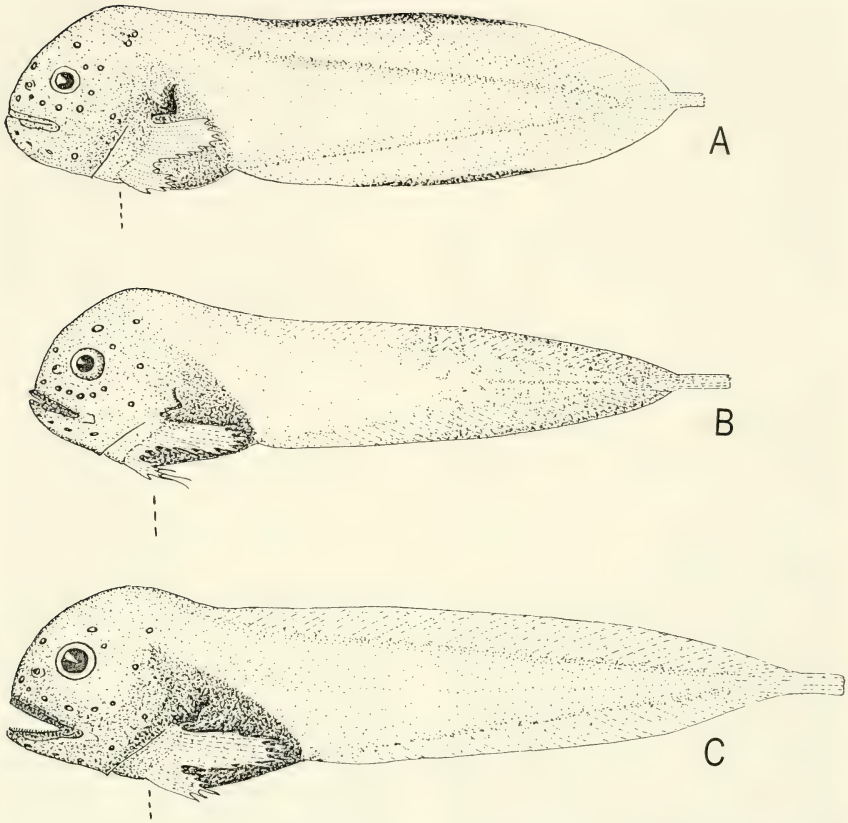

Figure 9. Three species of *Psednos*. (A) *P. gelatinosus* sp. nov. Juvenile, 30-mm standard length (SL). Holotype MCZ 64537. Southeast of Greenland, 0–650 m. (B) *P. groenlandicus* sp. nov. Male, 39.5-mm SL. Holotype ZMUC P 82660 (partially skinned; the black pigmentation along vertebrae is seen). Davis Strait, 930 m. (C) *P. harteli* sp. nov. Male, 48-mm SL. Holotype MCZ 63035. Western North Atlantic, 0–1008 m.

lar, sharply angled. The end of operculum directed posteriorly.

Pectoral fin 15(8+2+5) on left side and 15(8+1+6) on right side of holotype, 15(8+2+5) in two other specimens. Upper pectoral lobe 70(71)% HL, almost reaching anal-fin origin. Notch rays usually 2, short, about 30(25)% of upper lobe length. Lower lobe with thin elongate rays, about 70(88%) of upper lobe length. Pectoral fin located low, uppermost ray about level with posterior tip of oblique maxillary. Lowermost pectoral ray inserted a pupil diameter from prominent posterior tip of lower jaw (retroarticular process) and on a vertical with midpoint (⅓ in paratype) of postocular distance. Pectoral girdle of holotype (Fig. 8B) with 3 rounded radials.

Fenestrae in cartilaginous basal lamina absent. Scapula without a handlelike projection. Coracoid half-moon shaped.

Vertebrae 47(47), hemal spine of 11th vertebrae aligned with 1st anal-fin ray. Hemal spine present at least on 10th vertebrae. Interneural of 1st dorsal ray fits between neural spines of 4th and 5th vertebrae.

Sensory System. Coronal pore absent. Nasal pores 2, small and widely spaced, upper one opens behind vertical to nostril (level with nostril in holotype, but above it in paratype) and level with upper margin of eye. Infraorbital 6(5+1) on both sides of holotype and additional specimen and 4+1 pores on left side, 5+1 on right side in paratype. Temporal 1+1, t_1 pore large, longitudinally oval, twice size of io_6. Suprabranchial pore situated at a distance of 51(49)% HL from upper end of gill slit. Preoperculo-mandibular 6. Chin pores (pm_1–pm_1) spaced at a distance about equal to pm_1–pm_2.

Measurements and Counts. As percentage of SL: HL 24.8 (23.0), HW 14.7 (11.7), bd 28.6 (26.8), bdA 17.2 (14.7), preD 30.3 (26.4), preA 38.0 (33.8), mandanus — (18.9), anusA — (20.8), UPL 17.7 (16.0), notch 5.6 (4.0), LPL 13.4 (14.2), eye 5.1 (5.3), snout 8.1 (7.5), io 12.7 (10.9), postoc 14.6 (13.2), upj 12.6 (10.6), gsl 5.1 (5.5); as percentage of head length: HW 59.2 (50.8), bd 115 (116), bdA 69 (64), UPL 71.0 (70), eye 20.4 (23 0), snout 32.7 (32.8), io 51.0 (47.5), upj 51.0 (45.9), gsl 20.4 (23.8), postoc 59.2 (57 0). V 47(10+37), D 41, A 34–35, P 15(8+1–2+5–6), C 6. Radials 3. Gill rakers 7.

Color. Skin uniformly light but caudal part of body and especially margins of anal and dorsal fins with slight blackish pigmentation. In holotype, skin at end of caudal part of body damaged and a slight, but distinct, area of black pigmentation present along vertebrae, at least posteriorly, where skin is damaged. Pigment associated with bodies of vertebrae, very unusual for liparids. In paratype and additional specimen slight black pigmentation along vertebrae can also be seen in some places. Skin on snout and lower side of head unpigmented, only lips and edge of opercular flap are blackish. Surface of head below skin and gelatinous tissue dotted by black stellate melanophores, which are clearly seen through transparent skin. Dark color of head and belly is due to black mouth, gill cavity, and peritoneum. Midline of belly and lower lobe of pectoral fin with slight blackish pigmentation. Urogenital papilla pigmented. Stomach black. Pyloric ceca and anterior part of intestine a lighter dark dusky color. Reddish in life, body semitransparent; and a few milky-white spots present on lower jaw (P. R. Møller, personal communication).

Distribution. All 3 specimens caught southwest of Greenland (63°–65°N), in the Davis Strait at a depth of 930–1055 m.

Etymology. The name "groenlandicus" refers to Greenland waters, the type locality.

Comparative Notes. Psednos groenlandicus belongs to a group of *Psednos* with 47 vertebrae, no coronal pore, 6(5+1) io pores, and 6 preoperculo-mandibular pores. It is distinguished by its short mouth cleft reaching to below anterior margin of eye (upper jaw 10.6–12.6% SL), by an almost vertical and short gill slit about equal to eye. Pectoral notch usually has 2 rays, the caudal part of the body has slight blackish pigmentation near the end and along the vertebrae.

Most similar to *P. harteli*, which occurs more southward (ca. 40°N) but differs from it by elongate thin lower-lobe rays and 2 notch rays (vs thick handlike lower lobe and 1 notch ray), a short mouth (reaching to below anterior margin of eye vs pupil), a shorter upper jaw (10.6–12.6 vs 13.5% SL), a gill slit that is almost vertical (vs oblique), by peculiar pigmentation along vertebrae, and blackish pigment near end of caudal part of body (unpigmented in *P. harteli*). It also differs by a more compressed head (width 50–60 vs 70% HL), and by its black lips and mouth (vs brownish). *Psednos groenlandicus* dif-

fers from *P. christinae* by presence of only 6 (vs 7) pores in preoperculo-mandibular canal, unusual pigmentation along vertebrae, its short paddlelike (vs fingerlike) pyloric ceca, wider head (interorbital distance 47.5–51 vs 35–39% HL), dusky intestine (vs unpigmented); and scapula without handle (vs having a short, stout, anteriorly directed handle).

Psednos harteli new species

Hartel's Dwarf Snailfish (Figs. 5A, 6A, 9C)

Material. Holotype. MCZ 63035, adult male, 48 mm SL. 55 mm TL. R/V *Knorr*; Cr. 98. Western North Atlantic, 40°45′00″N, 65°03′00″W, 05 Oct. 1982. Multiple opening closing net, MOC 20-059,0. Depth 0–1008 m.

Diagnosis. A North Atlantic *Psednos* with V 47, D 42, no coronal pore, io 6(5+1), 6 preoperculo-mandibular and 1 suprabranchial pores, lower pectoral lobe wide and thick, handlike (Fig. 6A), 1 pectoral notch ray, gill slit distinctly oblique and short (about equal to eye), large mouth (cleft reaching to below pupil, upper jaw 13.5% SL), caudal part of body unpigmented.

Description. Body moderately humpbacked, depth at occiput 3.6 times in SL and 1.5 times depth at anal-fin origin. Trunk not long, preanal distance 38% SL. Dorsal and anal fins low and overlap half of caudal fin. Anus approximately on vertical at ½ postorbital distance, about midway between symphysis of lower jaw and anal-fin origin. Small thin urogenital papilla present. Skin transparent. Subcutaneous gelatinous layer weakly developed. Pyloric ceca not studied.

Head 4 in SL, wide, its width 70% HL and about 1.6 in head depth. Depth at occiput much greater than head length (112.5% HL). Anterodorsal profile of head rounded to tip of snout. Snout blunt, 1.4 eye diameter. Nostril level with eye center, small, about equal to diameter of nasal pore. Eye 4.8 in HL, pupil about ⅔ of eye diameter. Interorbital space wide, about 50% HL and 2.5 larger than eye. Subocular distance about equal to eye. Mouth terminal, moderately oblique forming about 30° angle to horizontal. Symphysis of upper jaw about level with midpoint of subocular distance. Mouth cleft reaching posteriorly to anterior half of pupil, maxillary reaching to below posterior margin of eye. Lower jaw included when mouth closed. Prominent tip of lower jaw (retroarticular process) on vertical at posterior edge of eye. Chin not deep, lower jaw not massive. Symphyseal knob absent. Teeth sharp, closely set in numerous oblique and curved rows, 6–7 teeth in row near symphysis in both jaws.

Gill slit about equal to eye diameter, completely above pectoral base and distinctly oblique. Dorsal end of gill slit below level of eye, ventral end almost level with posterior end of oblique mouth. Opercular flap small, triangular. End of operculum directed downward and level with lower third of subocular space.

Pectoral fin 14(8+1+5), with a wide, handlike lower lobe consisting of 5 thick rays united by membrane along more than half of their length (Fig. 6A) that is unique in *Psednos*. Width of lower lobe only slightly less than width of upper lobe. Upper lobe almost reaching anal-fin origin, its length 63% HL; 1 notch ray, about 26% of length of upper lobe. Pectoral fin situated low, uppermost ray level with posterior tip of oblique maxilla. Lowermost ray inserted about on a vertical with midpoint of postocular distance or ½ eye diameter behind prominent posterior tip of lower jaw.

Vertebrae V 47(11+36), hemal spine of 12th vertebrae aligns with 1st anal-fin ray. Hemal spines present also at least on 10th–11th vertebrae. Interneural of 1st dorsal ray fits between 5th and 6th vertebrae. Symphyseal knob clearly visible on radiographs of *P. micrurus*, *P. christinae*, and *Psednos* sp. 1 (Andriashev, 1992, fig. 3) not present in this species (Fig. 5A).

Sensory System. Coronal pore absent. Nasal 2, n_2 pore as large as nostril and open far above nostril and level with upper margin of eye. Infraorbital 6(5+1), io_{1-5}

pore in a line below eye; io_6 pore opens behind upper margin of eye. Pore t_1 large, longitudinally oval and 2 times diameter of io_6. Temporal 1+1; suprabranchial pore about ½ HL from dorsal end of gill slit. Preoperculo-mandibular 6, pm_6 pore about level with eye center. Chin pores spaced at a distance equal to pm_1–pm_2. The pm_2–pm_4 pores slightly enlarged, oval.

Measurement and Counts. HL 25.0, HW 17.7 (70.8), bd 28.1 (112.5), bdA 18.8 (75), preD 31.2, preA 41.7, mand-anus 20.8, anusA 20.4, UPL 15.6 (62.5), notch 4.2, LPL 11.0 (70% UPL), eye 5.2 (20.8), snout 7.3 (29.2), io 12.9 (51.7), postoc 14.2 (56.7), upj 13.5 (54.2), gsl 5.2 (20.8). V 47(11+36), D 42, A 35, P 14(8+1+5), C 6.

Color. Skin uniformly light, caudal part of body without any sign of dark pigmentation. Head and belly look dark because of the pigmentation of mouth, gill cavity, and peritoneum. Skin light on snout and lower side of head. Lips light brownish. Color of internal organs not studied.

Distribution. The only specimen was caught above the continental slope of eastern North America (about 40°N), at a depth of 0–1008 m.

Etymology. The new species is named for the American ichthyologist Karsten Edward Hartel of the Museum of Comparative Zoology, Harvard University.

Comparative Notes. Psednos harteli belongs to a group of *Psednos* with 47 vertebrae, no coronal pore, 6(5+1) io pores, and 6 preoperculo-mandibular pores. It is distinguished by its thick, handlike lower pectoral lobe, a distinctly oblique gill slit, a wide head (70% HL), and an unpigmented caudal part. It is the most similar to *P. groenlandicus* (see above). *Psednos harteli* differs from the sympatric, but deeper-living (1042–1368 m) *P. barnardi*, by a larger eye (21 vs 17.8% HL), an oblique (vs almost vertical) gill slit equal to eye diameter (vs 1.7) that is located low (its dorsal end is below level of eye vs level with pupil), a larger mouth cleft reaching almost to eye center (vs anterior margin of eye), dark brown peritoneum (vs bluish-black), and light skin on chin and lower jaw (vs black). *Psednos harteli* differs from *P. christinae* in number of preoperculo-mandibular pores (6 vs 7), a handlike lower pectoral lobe, wider head (70 vs 53% HL), wider interorbital (52 vs 35–39% HL), rounded (not straight) anterodorsal profile, a longer upper jaw (54 vs 42–46% HL), and larger preanal distance (42 vs 34–36% SL). In addition, the body is less humpbacked; the depth at occiput 1.5 (vs 2) times the depth above anal-fin origin and the lowermost pectoral ray is inserted on vertical at about the middle of postocular distance (just behind a vertical to eye in *P. christinae*).

Psednos microps new species

Smalleye Dwarf Snailfish (Figs. 3C, 10A)

Psednos microrus (non Barnard, 1927): Stein, 1979: 6, fig. 1 (ex parte: 1 of 2 specimens, USNM 200520; Indian Ocean).

Material. Holotype. USNM 200520, juv. female, 18 mm SL. R/V *Anton Bruun*, Sta. 7105. SW Indian Ocean, Crozet Basin, 35°02′S, 60°01′E, 9 Sep. 1963. Isaacs-Kidd midwater trawl, depth 275–2275 m.

Diagnosis. An Indian Ocean *Psednos* with V 41, D 37, coronal pore present, 1st temporal and 6th infraorbital pores absent, very small eye (13% HL), low gill slit, superior mouth, and pale skin.

Description. Depth at occiput 3.4 times in SL and 1.8 times greater than depth at anal-fin origin. Trunk rather long, preanal distance 44.4% SL. Anus located just behind base of lower pectoral lobe, about at vertical to midpostocular distance. Caudal rays missing.

Head large, 3.3 in SL and compressed, width 57% HL or 1.8 times in depth. Depth at occiput equal to head length. Anterodorsal profile slopes abruptly anteriorly but is concave above eye. Snout 2 times eye diameter. Nostril small, located high, slightly above level of upper eye margin. Eye very small, 7.6 times in HL. Mouth superior, forming angle 50–60° to horizontal. Symphysis of upper jaw level with upper margin of eye. Lower jaw pro-

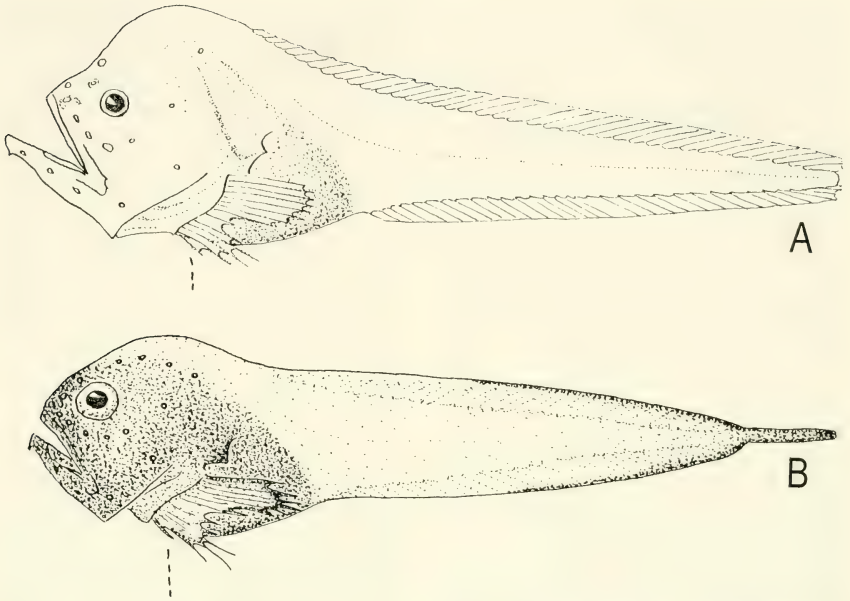

Figure 10. Two species of *Psednos*. (A) *P. microps* sp. nov. Juvenile, 18-mm standard length (SL). Holotype USNM 200520. Caudal rays missing. Pectoral fin length unknown. Indian Ocean, Crozet Basin, 275–2275 m. (B) *P. micruroides* sp. nov. Male, 31-mm SL. Holotype MCZ 64538. Southeast Greenland, 0–900 m.

jecting. Mouth cleft not reaching vertical with nostril, maxilla reaching vertical to anterior margin of pupil. Symphyseal knob present. Teeth sharp, about 5 in each row near symphysis of lower and upper jaws. Chin low, lower jaw not massive. Prominent tip of lower jaw (retroarticular process) angled at about 90° and on vertical with anterior margin of pupil.

Gill slit 1.4 eye diameters, completely above pectoral base and slightly oblique. Dorsal end of gill slit level with upper ⅕ of subocular distance, ventral end level with posterior end of oblique mouth. Opercular flap very small, triangular. End of operculum directed posterodorsally, its tip reaching midsubocular level.

Pectoral fin 14(8+1+5) with 1 notch ray that is clearly separated from neighboring rays. Uppermost pectoral ray level with posterior end of oblique mouth cleft, base of lowermost ray on vertical at ⅓ postocular distance.

Sensory System. Nasal pores 2, located high; n_1 pore level with nostril and above level of upper margin of eye; n_2 pore about 3 times larger than nostril and above eye by about a pupil diameter. Coronal pore present, equal in size to n_2 pore. Temporal pores 0+1 (the t_1 pore, usually above eye, absent); suprabranchial pore 40% HL from dorsal end of gill slit. Infraorbital 5+0 (the io_6 pore, usually behind upper margin of eye, absent). The io_1 pore on top of prominent projection of anterior suborbital bones and level with upper ½ of eye. Preoperculo-mandibular pores 6, pm_6 pore level with eye center. Chin pores (pm_1–pm_1) spaced at ⅔ of distance between pm_1–pm_2.

Measurements. HL 29.4, HW 16.7 (57), bd 29.4 (100), bdA 16.7 (57), preD 26.1, preA 44.4, mand-anus 25.0, anusA 25.0, pectoral rays broken, snout 7.8 (26.4), upj 16.1 (55), eye 3.9 (13.2), postoc 18.3 (62.3), io 12.8 (43.5), gsl 5.6 (18.9). V 41(10+31), D 37, A 30, P 14(8+1+5), C 6.

Color. Body pale, caudal part of body unpigmented. Peritoneum and gill cavity brown and clearly seen externally.

Etymology. The name "microps" in Greek refers to the small eyes of this species.

Distribution. Known only from the Crozet Basin in the southwestern Indian Ocean, at a depth 275–2275 m.

Comparative Notes. Psednos microps belongs to a species group with 41–43 vertebrae, a coronal pore, and 5(5+0) io pores. Unusual by absence of 1st temporal pore. Distinguished by very small eye (13% HL), superior mouth, low gill slit, and pale color. It differs from *P. steini* sp. nov., the only congener from the Indian Ocean, by absence of 1st temporal pore, the longer head (29 vs 24.5% SL), very small eye (7.6 vs 3.6 times in HL). Symphysis of upper jaw level with upper margin of eye (vs with lower ½ of eye), and accordingly higher nostril and n_1, n_2 io_2 pores (nostril and n_2 above eye vs level with eye center and its upper margin), and a gill slit and pectoral fin that are located lower. Occurs at greater depth (275–2275 vs 0–350 m).

If allometric growth of *P. microps* is similar to that of *P. barnardi*, one can assume that adult *P. microps* might have smaller heads (ca. 25% SL) and larger eyes (ca. 19% HL) and resemble *P. steini*; nevertheless, differences (absence of t_1 pore, high position of nostril and n_1, n_2, io_1 pores, and low location of gill slit and pectoral fin) clearly separate the species.

Psednos micruroides new species

Multipore Dwarf Snailfish (Figs. 2, 3A, 5C, 10B)

Material. Holotype. MCZ 64538. Subadult male, 31 mm SL, 36.5 mm TL. R/V *Endeavor*, Cr. 133. Off south-east Greenland, 63°50′18″N, 35°40′30″W, 13 Aug. 1985. 13.08.1985. EN 133-17. Depth 0–900 m. Coll. David Backus.

Diagnosis. A North Atlantic *Psednos* with V 43, D 38, coronal pore present, 6th infraorbital pore absent, 3–4 pores in temporal canal; eye 22.7% HL, mouth terminal, and gill slit equal to eye diameter.

Description. Depth at occiput 3.7 times in SL or about 2 times depth at anal-fin origin. Trunk rather large, preanal about 45% SL. Dorsal and anal fins low, overlaping ¼ of caudal fin. Anus on vertical with midpoint of postocular distance. Urogenital papilla present. Skin transparent. Gelatinous subcutaneous tissue weakly developed. Pyloryc ceca not studied because belly not dissected.

Head large, 3.5 times in SL and quite compressed, width about 60% HL or 1.5 in head depth. Depth at occiput slightly less than head length (96% HL). Anterodorsal profile sloping to tip of snout. Snout blunt, about equal to eye diameter. Nostril about ½ pore diameter, level with eye center. Eye 4.4 times in HL, pupil about ⅔ of eye. Interorbital 46% HL and 2 times larger than eye. Mouth terminal, oblique, forming 55–60° angle. Symphysis of upper jaw about level with lower margin of eye. Lips thin, posterior ½ of lower lip with lateral lobe. Mouth cleft reaching posterior to vertical at anterior margin of eye, maxilla reaching posterior margin of pupil. Lower jaw included. Symphyseal knob well developed. Chin low, lower jaw not massive. Prominent tip of lower jaw (retroarticular process) on vertical with posterior margin of eye. Teeth small, in a few oblique rows, about 3–4 per row near symphysis of both upper and lower jaws.

Gill slit oblique, equal to eye diameter, completely above pectoral base; dorsal end slightly below the level of lower margin of eye. Opercular flap triangular. End of operculum directed posteroventrally and level with posterior end of oblique mouth.

Pectoral fin 13(7+1+5) with 1 notch ray, its length about 30% of upper lobe length. Upper pectoral lobe not reaching

anal-fin origin. Lower lobe with 5 thin rays, longest about 84% of upper lobe length. Pectoral fin located low, upper ray level with posterior end of oblique mouth. Lowermost pectoral ray inserted on vertical at midpoint of postocular distance or about ¾ of eye diameter from prominent posterior tip of lower jaw.

Vertebrae 43(11+32), hemal spine of 12th vertebrae aligned with 1st anal-fin ray. Hemal spines present at least on 10th–11th vertebrae. Interneural of 1st dorsal ray fits between 4th and 5th neural spines.

Sensory System. Coronal pore present. Nasal pores 2, upper level with upper margin of eye. Infraorbital 5(5+0) on left side, 4(4+0) on right side, small, about equal in size and situated on a curved line below eye; io_6 pore absent. Left temporal canal with 4 pores, right with 3 (Fig. 2). Pore t_1 situated above posterior margin of eye, small; t_2, t_3, and t_{sb} in 1 line and t_{sb} pore 36% HL from upper end of gill slit. Preoperculo-mandibular pores 6, pm_6 pore level with eye center. Chin pores small, interspace between pm_1 and pm_1 slightly less than distance between pm_1 and pm_2.

Measurements and Counts. HL 28.4, HW 17.7 (62. 5), bd 27.1 (95.4), bdA 13.9 (40), preD 32.3, preA 45.2, mand-anus 24.2, anusA 25.8, UPL 16.1 (56.0), notch 4.8, LPL 13.5, eye 6.5 (22.7), snout 6.5 (22. 7), io 12.9 (45.5), postoc 16.8 (59.2), upj 12.9 (45.5), gsl 6.5 (22.7). V 43(11+32), D 38, A 30, P 13(7+1+5), C 6.

Color. Head and belly dark, body pale, margins of vertical fins and margins of upper and lower pectoral lobes darkly pigmented. Skin on snout, lips and lower jaw, mouth and gill cavity, and margins of opercular flap brownish-black. Peritoneum brownish-black and clearly seen externally. Lower pectoral rays blackish. Color of internal organs not studied.

Distribution. The only known specimen caught in midwater southeast of Greenland at a depth of 0–900 m.

Etymology. The name *micruroides* is a derivative of Barnard's original specific name, *micrurus*, and is used because of the similarity between the two species.

Comparative Notes. Psednos micruroides belongs to a group of *Psednos* with few vertebrae (41–43), a coronal pore, but 6th infraorbital pore absent. It differs from all others species of this group by presence of 3–4 temporal pores in a row. It is also distinguished by its large head (28.4% SL), a gill slit equal to eye, and color pattern. Few vertebrae and the presence of a coronal pore make it similar to *P. micrurus* (see below). However, *P. micrurus* has 17 pectoral rays (vs 13), pectoral fin is not divided into 2 lobes (vs distinctly bilobed with an obvious notch), and the lower pectoral rays are longer than the upper ones (vs the lower lobe shorter than the upper). Also, the maximum body depth in *P. micrurus* clearly exceeds head length (138% HL) but in *P. micruroides* it is slightly less than head length (96%). *Psednos micrurus* has a short head (22.2% SL) and the upper pectoral lobe is greater than head length, whereas in *P. micruroides* the head is much larger (28% SL) and the upper pectoral lobe is less than head length (about 60% HL). The head of *P. micrurus* is very compressed and equal to about 0.5 HL (Andriashev, 1992: 8) and the teeth in lower jaw have two teeth per row near symphysis. In *P. micruroides* the head is wider (63% HL) and the teeth in the lower jaw are 3–4 per row.

Psednos micrurus Barnard, 1927

Barnard's Dwarf Snailfish (Fig. 11)

Psednos micrurus Barnard, 1927a: 76; 1927b: 927, pl. 33, fig. 5 (off Cape Point, South Africa, 660–700 fath.). Holotype: BMNH 1930.1.14.7. Ovigerous female SL 45 mm; bad condition in 1992. Paratype disintegrated (see Andriashev, 1992). Andriashev, 1986: 107 (ex parte: sec Barnard, 1927); 1992: 4, figs. 2, 3a; 1993a: 7, fig. 2B (ex parte: redescription of the holotype).

Paraliparis micrurus (non Barnard, 1927): Stein, 1979: 6, fig. 1. 1986a: 494 (Indian Ocean).—Andriashev, 1986: 107, fig. 48; 1992: 4, fig. 1; 1993a: 7, fig. 1 (ex parte: sec Stein, 1979).

Material. Radiograph (ZISP 17451) of the holotype and pectoral girdle preparation no. 544, *Psednos* cf.

micrurus ZISP 51704, SL 13 mm, TL 14.5 mm. Madagascar Ridge, 31°18′S, 46°05′E, R/V *Vityaz*, Sta. 2773, 25 Dec. 1988, at a depth 1000–0 m over bottom at 2600-2100 m.

Diagnosis. A *Psednos* from off South Africa with V 43, coronal pore present; pectoral unnotched; head short (22% SL), preanal large (50% SL), teeth on lower jaw in double row, color grayish-brown.

Description. This description is a combination of Barnard's original description (1927), redescription of the holotype (Andriashev, 1992: 6, figs. 2, 3a), and my observations. Trunk long, preanal distance about equal to half of standard length. Pyloric ceca 5, equally short and thick. "Mouth very oblique, lower jaw projecting .... Caudal completely confluent with dorsal and anal. Vent between lower extremities of pectorals .... Resembling *Amitra* (=*Paraliparis liparinus*) in the pectoral" (Barnard, 1927a: 76). "Maxilla reaching to below anterior third of eye. Distance from snout to origin of dorsal nearly twice, to origin of anal fin 2 and ⅓ times, length of head. P 17, rays at least as long as head, the lower rays probably slightly longer .... Length up to 45 mm. Grayish brown (as preserved). The type has the body cavity filled with a number of large eggs, 1 mm in diameter. Another specimen of the same size is rather badly mutilated, but confirmed the above characters" (Barnard, 1927a: 77).

Andriashev (1992: 6, figs. 2, 3a) noted the following. Outer outline of head rises abruptly from short snout to highly rounded occiput and then tapers more gently to thin caudal part of body. Head very compressed, its width equal to about ½ of head length. Depth at occiput is 2 times as high as that at anal-fin origin. Snout not projecting, blunt, rostral fold not developed. Lips thin. Mouth distinctly superior, strongly oblique; upper jaw forms an angle about 50–60° to horizontal midline of body. Lower jaw projecting, with a symphyseal knob. Teeth in jaws very small, simple, sharpened; those in lower jaw form a narrow band consisting of an irregular double row. Posterior end of the lower jaw forms a distinct ventrally directed angle. Eye round, large, about 4 times in head length.

Sensory Pores. Few pores have been noted on the holotype. Andriashev (1992: 8) found: "Pores of infraorbital canal are in line under eye. Remains of small canal behind eye are discernible with the terminal pore io_6 that may evidence of an interruption of the infraorbital canal behind eye; trace of suprabranchial pore widely spaced from the upper margin of gill opening may be descerned .... Nasal pores and a coronal one are not discernible because of a damaged skin." Coronal pore always present in *Psednos* with few vertebrae (41–43) so it is probably present in *P. micrurus*. The reconstruction of pores by Andriashev (1992, p. 9, fig. 1), based on figure 1 in Stein (1979) belongs to another species (see below *P. steini* sp. nov.).

Pectoral girdle (based on Andriashev, 1992, fig. 2) has 3 rounded and almost equally spaced radials; lower radial largest and ½ again as large as upper radials. Cartilaginous basal lamina without fenestrae. Scapula probably without a handlelike projection, coracoid with the short, rather thick, anteriorly directed projection. Pectoral fins very damaged and only a few rays remain, at least 13–14 in one fin.

"Parapophyses of three posterior abdominal vertebrae are probably joined together forming a gradually elongated haemal spines; the longest spine is on the 12th vertebra but only the haemal spine of 13th vertebra fits to the 1st anal ray; thus number of vertebrae is probably 12 abdominal (9+3) and 31 (30+1, as urostyle vertebra lost) caudal vertebrae, totaling 43. Number of caudal rays is unknown. Interneural of the 1st dorsal ray fits between 5 to 6th neural spines" (Andriashev, 1992: 9).

Counts. V 43, D ca. 37, A ca. 30. P damaged but at least 13–14, Barnard (1927a, b) counted 17. C. unknown.

Color. "Body is uniformly pale, greyish; peritoneum dark brown dorsally; esophagus pigmented intensively, blackish-brown;

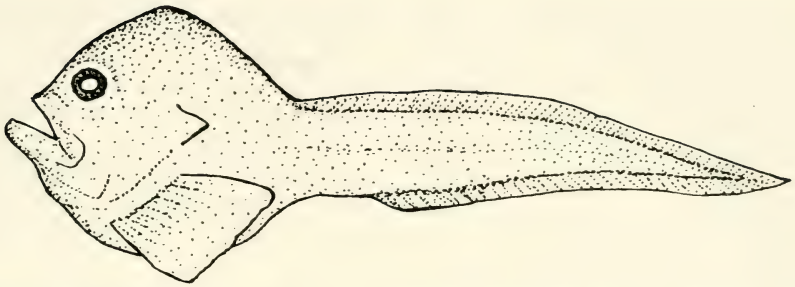

Figure 11. *Psednos micrurus* Barnard. Female, 45-mm standard length. Holotype BMNH 1930.1.14.7 (after Barnard, 1927b). South Africa, 1208–1280 m.

stomach and pyloric caeca light brown because of scarce melanophores, adjacent part of intestine blackish, the rest of intestine not pigmented except of short part near anus" (Andriashev, 1992: 9).

Distribution. Only known from off Cape Point, South Africa, at a depth of 1208–1280 m. Other Indian Ocean specimens cited by Stein (1979) belong to other species (see *P. steini* sp. nov. and *P. microps* sp. nov). However, the species may range north to the Madagascar Ridge based on a 13-mm-SL juvenile in poor condition (ZISP 51704) that is similar to *P. micrurus*. This specimen has V 42(10+32), D 37, A 30, C 6. Interneural of 1st dorsal ray fits between 4th and 5th vertebrae. In percentage of SL: preD 36.9, preA 50, bd 25.4 (studied in 1992 by A. Andriashev). It is similar to *P. micrurus* in meristic counts and large preanal but differs from it by absence of pyloric ceca (vs 5 in *P. micrurus*).

Comparative Notes. Psednos micrurus belongs to the group of *Psednos* with few vertebrae (41–43). It differs from other species of the group by a long preanal distance (ca. 50 vs 38.5–45% SL), a short head (22 vs 24.5–29.5% SL) that is very compressed (width 50% HL), teeth on lower jaw in double row, grayish-brown color, and unnotched pectoral fin. Unnotched pectoral fins (without a short notch ray but with the lower lobe rays longer than upper) as described for *P. micrurus* by Barnard (1927a,b) are unusual in liparids. However, it is a valid character and is found in *Paraliparis challengeri* and in the related *P. liparinus* (Andriashev, 1993b). It is impossible to check this character in *P. micrurus* because the holotype is in bad condition (Andriashev, 1992) but Barnard (1927a,b) stated that the pectoral fin of *P. micrurus* is similar to the unnotched fin of another liparid, *Amitra liparina* Goode, 1881 (synonym of *Paraliparis liparinus*). Stein (1979) doubted the character in citing Burke (1930: 170), who had redescribed Goode's species and found its pectoral fin deeply notched. At the time of Stein's comment it was not known that Burke based his redescription of *Amitra* (=*Paraliparis*) *liparina* on specimens belonging to another species. Andriashev (1993b) later stated that the unnotched pectoral fin is a unique and remarkable diagnostic character for *P. liparinus* (Goode, 1881). Thus an unnotched pectoral fin with elongated lower rays is a valid character in Liparidae and is probably the most distinguishing feature for *P. micrurus*.

Psednos mirabilis new species

Marvellous Dwarf Snailfish (Figs. 12A, 13A)

Material. Holotype. MCZ 155423, unripe male SL 28 mm. R/V *Delaware II*, Sta. 15. Slope off New England, 39°47′N, 70°39′W, 4 Feb. 1999, DE 99-02: 015, 0–700 m over bottom at 1370–1700 m.

Diagnosis. A *Psednos* from the North Atlantic with V 41, D 34, coronal pore present, temporal pores 1+1, large gill slit (47% HL or 2 eye diameters); P 13(8+0+5), no notch ray; large head (29.4% SL), eye 21.2% HL, head and belly black, caudal part of body light, margins of dorsal and anal fins with narrow blackish pigmentation.

Description. Body only slightly humpbacked, depth at occiput 1.6 times greater than depth at anal-fin origin. Maximum depth (at occiput) 3.6 times in SL. Preanal about 46% SL. Dorsal and anal overlap 36% of caudal fin. Anus close to base of lower lobe of pectoral fin. Gelatinous subcutaneous tissue weakly developed.

Head long (3.3 in SL), wide (1.3 in head depth or about 70% HL). Depth at occiput almost equal to head length (92% HL), anterodorsal profile of head only slanted slightly anteriorly. Snout blunt and wide, 1.4 eye diameters, its tip located high, almost level with upper margin of eye. Nostril located high, level with upper margin of eye, about half diameter of upper nasal pore. Eye 4.7 in HL, pupil ⅔ eye diameter. Interorbital 2.2 times eye. Mouth superior, almost vertical. Lower jaw included. Teeth 3–4 and 2–3 per row near symphysis of upper and lower jaws, respectively. Symphyseal knob present.

Gill slit large, about 2.2 eye diameters, very oblique, and entirely above pectoral base; its dorsal end below level of eye. Opercular flap triangular, operculum directed posteroventrally, tip level with posterior end of oblique mouth.

Pectoral fin 13(8+0+5), lacking notch ray (uncommon in *Psednos*). Lower lobe with 5 rays clearly separated from upper lobe. Upper lobe rays short (about 47% HL), not reaching to anal-fin origin. Lower pectoral lobe about 88% of upper lobe length. Pectoral fin low, uppermost ray about level with posterior end of oblique mouth. Pectoral girdle (Fig. 13A) with 3 rounded, equally spaced radials. Basal cartilaginous lamina without fenestrae. Scapula without a handlelike projection. Coracoid damaged.

Vertebrae 41(10+31), vertebral column not highly curved anteriorly. Interneural of 1st dorsal ray fits between neural spines of 5th and 6th vertebrae.

Sensory System. Coronal pore present, nasal pores 2, infraorbital 5(5+0), temporal 1+1, preopercule-mandibular 6. Pores n_1, n_2, and io_1 high: io_1 level with upper margin of eye, with n_1 and n_2 pores clearly above it.

Measurements and Counts. HL 29.4 HW 21.4 (71), bd 27.9 (92), bdA 17.9 (59), preD ca. 32.1, preA ca. 46.4, UPL 14.3 (47), LPL 12.5, snout 8.9 (29.4), eye 6.4 (21.2), postoc 17.1 (56), io 14.3 (47), upj 12.1 (40), gsl 14.3 (47). V 41(10+31), D 34, A 29, P 13(8+0+5), C 6. Radials 3.

Color. Head and belly appear black, caudal part of body pale. Dorsal, anal, and caudal fins with narrow blackish margin. Pectoral fin pale with blackish pigmentation along rays. Peritoneum, mouth, and gill cavity black. Skin on head transparent, head muscles densely pigmented under the skin with black melanophores that are clearly seen externally. Anal area black. Stomach black.

Distribution. Known only from the slope off southern New England in the western North Atlantic (about 40°N), over bottom at a depth of 1370–1700 m.

Etymology. Named "mirabilis" (Lat.), which means amazing or marvelous.

Comparative Notes. Psednos mirabilis belongs to the group of *Psednos* with few vertebrae (41–43), a coronal pore, 5(5+0) io pores, and 1+1 temporal pores. Distinguished by large gill slit (47% HL or 2 eye diameters), pectoral notch lacking a notch ray, long head (29.4% SL), and color pattern. It is most similar to *P. micruroides* but differs in having 2 widely spaced temporal pores (vs 3 or 4 in a row), a large gill slit (47 vs 23% HL, or twice as large as eye vs equal to eye), comparatively short pectoral fin (47 vs 56% HL) that lacks a notch ray, by different pectoral ray counts P 8+0+5 (vs 7+1+5), a more vertical

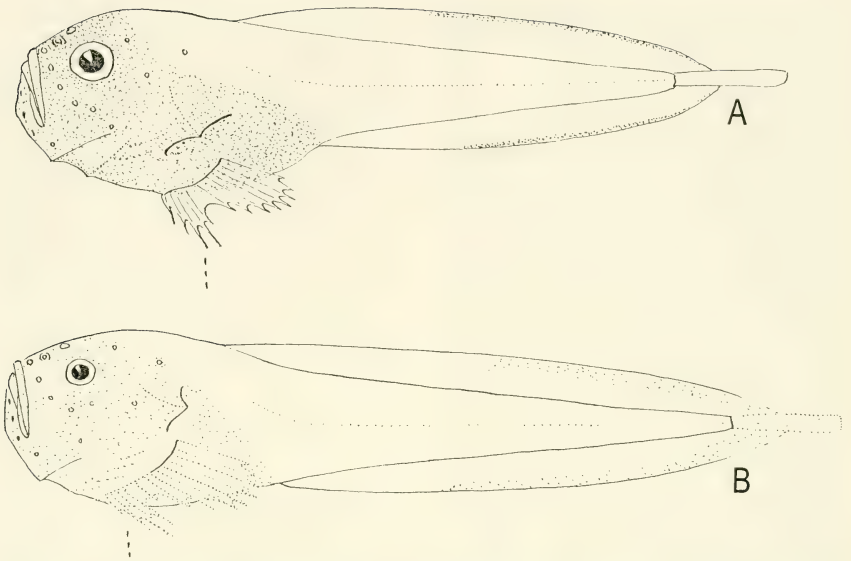

Figure 12. Two species of *Psednos*. (A) *P. mirabilis* sp. nov. Male, 28-mm standard length (SL). Holotype MCZ 155423. Slope off New England, 1370–1700 m. Position of gill slit and pectoral fin shown approximately. Anterior nasal pore not seen. (B) *P. sargassicus* sp. nov. Female, 52-mm SL. Holotype. MCZ 89997. Northern Sargasso Sea, depth 0–1050 m. Position of gill slit and pectoral fin, length of its rays and caudal fin shown approximately. Anterior nasal pore not seen.

mouth, and by the high location of the tip of snout, nostril, and snout pores. It is caught at a greater depth, 1300–1700 (vs 0–900) m.

Psednos sargassicus new species

Sargasso Dwarf Snailfish (Figs. 12B, 13B)

Material. Holotype. MCZ 89997. Adult female 52 mm SL. R/V *Atlantis II*, Cr. 71. Northern Sargasso Sea, 35°30′N, 67°14′30″W. 26 Sep. 1972. Depth 1050–0 m. Coll. A. E. Jahn.

Diagnosis. A *Psednos* from the North Atlantic with V 42, D 37, coronal pore present, io 5(5+0), temporal 1+1, head 25% SL, eye small (15.3% HL), gill slit located high (dorsal end about level with eye center), preanal short (38.5% SL), pectoral fin with 1 notch ray; caudal part of body pale; head, belly, and margins of vertical fins brown.

Description. Body slightly humpbacked, depth at occiput 4.3 in SL or 1.8 times depth at anal-fin origin. Trunk not long, preanal 38.5% SL. Anus located behind base of lower pectoral lobe.

Head 4 times in SL, compressed (width 1.7 in head depth or 54% HL). Depth at occiput 92% HL, anterodorsal profile only slightly slanted anteriorly. Snout blunt and wide, length 1.9 eye diameters; tip of snout high, almost level with upper margin of eye. Nostril small, about ½ diameter of upper nasal pore, level with upper margin of eye. Eye small, 6.5 times in HL. Interorbital 2.6 times greater than eye. Mouth very oblique, almost vertical. Teeth about 5–6 and 4–5 per row near symphysis upper and lower jaws, respectively. Wide upper jaw diastema.

Gill slit 1.5 eye diameters, completely above pectoral base, dorsal end about level

with eye center. Opercular flap triangular. Operculum posteriorly directed, end slightly below level of eye.

Pectoral girdle (Fig. 13B) with 3 large, equally spaced radials. Cartilaginous basal lamina without fenestrae. Scapula crescent-shaped, handlelike projection entirely fused with body as evident by remnant anterior fenestrae covered by thin bone. Coracoid half-moon shaped, handlelike projection entirely fused with body by means of thin riblike bone (lamellae); an unusual tiny hole present on body. Pectoral fin 15(9+1+4), with 1 notch ray. Length of lower lobe and notch rays unknown because of damage. Uppermost pectoral ray about level with posterior end of oblique mouth.

Vertebrae 42(10+32). Interneural of 1st dorsal ray fits between neural spines of 4th and 5th vertebrae.

Sensory System. Coronal pore present, nasal 2, infraorbital 5(5+0), temporal 1+1, preoperculo-mandibular 6. Snout pores located high: io_1 and n_1 level with upper margin of eye, n_2 above it.

Measurements and Counts. HL 25, HW 13.5 (54), bd 23 (92), bdA 19.2 (52.3), preD ca. 28.8, preA ca. 38.5, snout 7.3 (29.2), eye 3.8 (15.4), postoc 14.2 (57), io 10.2 (40.8), gsl 3.8 (15). V 42(10+32), D 37, A 31, P 15(9+1+4), C 6 (?). Radials 3, rounded.

Color. Head and belly dark brown, caudal part of body pale (partially lacking skin at end). Peritoneum, mouth, and gill cavity dark brown. Margins of dorsal and anal fins and anal area brown. Snout light brown, suprabranchial pore bordered with brown.

Distribution. Only known from the northern Sargasso Sea in the North Atlantic (about 35°30′N) at a depth of 0–1050 m.

Etymology. Named "sargassicus" in reference to type locality, the Sargasso Sea.

Comparative Notes. Psednos sargassicus belongs to the group of *Psednos* with few vertebrae (41–43), a coronal pore, 5(5+0) infraorbital pores, and 1+1 temporal pores. Distinguished by a small eye (15.3% HL), gill slit located high (dorsal end almost level with eye center), and short preanal (38.5% SL). Also, pectoral fin has 1 notch ray; and head 25% SL. Caudal part of body pale, but head, belly, and margins of vertical fins brown. Most similar to *P. mirabilis* but differs in having a smaller eye (15.4 vs 21.2% HL), short gill slit (15 vs 47% HL or 1.5 vs 2.2 eye diameter) located high (its dorsal end level with eye center vs below eye level), pectoral notch with 1 ray (vs without a ray), and color is brown not black.

It shares a small eye with *P. microps* of the Indian Ocean but differs from it in having an anterior temporal pore, t 1+1 (vs t 0+1), smaller head, higher gill slit, a less humpbacked body, and by brown margins on vertical fin (vs unpigmented).

Psednos steini new species

Stein's Dwarf Snailfish (Fig. 13)

Paraliparis micrurus (non Barnard, 1927): Stein, 1979: 6, fig. 1 (ex parte: one of two specimens, USNM 200488; Indian Ocean, 2600 miles east of the Cape of Good Hope).

Psednos micrurus (non Barnard, 1927): Andriashev, 1986: 107, fig. 48; 1992: 9, fig. 1; 1993a: 9, fig. 1 (ex parte: figure after Stein, 1979, and explanation of pores depicted).

Material. Holotype. USNM 200488. Adult male, 37 mm SL. R/V *Anton Bruun*, Sta. 351 C. South-west Indian Ocean, 31°35′S, 65°08′E, 28/29 Jun. 1964, depth 0–350 m over 1428 m. Now disintegrated.

Diagnosis. An Indian Ocean *Psednos* with about 43 vertebrae, D 36, coronal pore present, temporal pores 1+1; pectoral fin 14(8+1+5), with 1 notch ray; eye not less than 20% HL, gill slit equal to eye and vertical, its dorsal end level with pupil; color tan.

Description. This new species is based on 1 of 2 *Psednos* specimens described from the Indian Ocean by Stein (1979), which he treated under the name *Paraliparis micrurus*. The specimen is now disintegrated, but Stein's text and figure (Stein, 1979) are excellent and they form the basis of this description. Characters

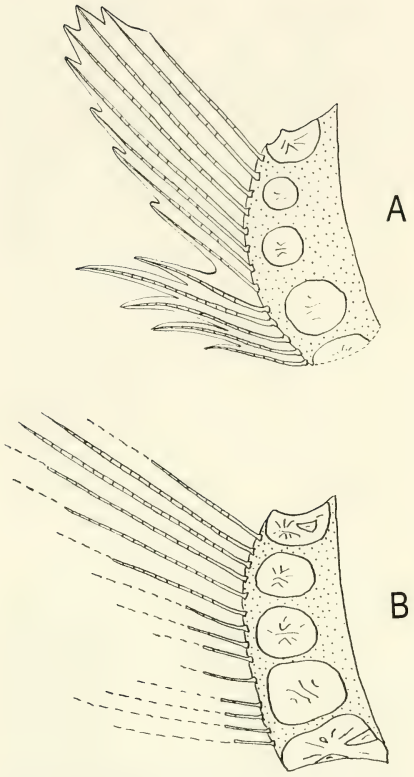

Figure 13. Right pectoral girdle and fin of two *Psednos*. (A) *P. mirabilis*. Holotype. Coracoid damaged. (B) *P. sargassicus*. Holotype. Length of lower lobe and notch rays unknown.

and measurements based on Stein's figure are placed in square brackets.

Body humpbacked, [depth above occiput 3.9 times in SL or 2.3 greater than depth at anal-fin origin]. Trunk rather long, preanal 43.6% SL. [Dorsal and anal fins overlap ½ of caudal]. Anal-fin origin below about 8th dorsal-fin ray. Anus between bases of lower pectoral-fin lobes. Small urogenital papilla present [in male]. Pyloric ceca short, flat, and blunt.

Head 4.1 in SL, width unknown. Depth at occiput slightly larger than head length (107% HL), anterodorsal profile evenly sloping, slightly concave. Snout about equal to eye diameter. Nostril with slightly raised rim [level with eye center]. Eye 3.6 times in HL. Mouth superior, distinctly oblique, forming an angle of about 50° to horizontal. [Symphysis of upper jaw level with eye center.] Maxillary reaching vertical at anterior ½ of eye [mouth cleft to vertical at nostril]. Symphyseal knob present. "Teeth in both jaws simple, moderately stout, slightly recurved. Upper jaw teeth in irregular oblique rows forming narrow band less than four teeth wide, uniserial posteriorly; mandibular teeth in about 13 oblique rows forming band similar to upper jaw. Suborbital bones extend anteriorly forming distinct projections above snout on either side of upper jaw" (Stein 1979: 7). [Chin low, lower jaw not massive. Prominent tip of lower jaw (retroarticular process) angled at ca. 90° and on vertical to posterior margin of eye.]

Gill slit [vertical, about equal to eye diameter], completely above pectoral fin base [dorsal end level with lower margin of eye; ventral end level with lower ⅓ of subocular space]. Opercular flap small triangular [operculum posteroventrally directed, tip level with upper ⅓ of subocular space].

"Pectoral fin moderately deep notch; uppermost ray on horizontal line between posterior corner of maxillary and lower margin of orbit. Upper lobe of eight closely spaced rays, separated from five closely spaced lower lobe rays by a single short ray in notch, distinctly separated from rays above and below it. Origin of ventralmost pectoral rays about below posterior margin of interopercle" (Stein 1979: 7). Pectoral fin 14(8+1+5). [Pectoral fin short, length of upper lobe ca. 56% HL, tip not reaching anal fin origin. Lower pectoral lobe shorter than upper one. Base of lowermost ray on vertical at ¾ of postocular distance. Upper ray level with lower ⅓ of subocular space.]

Vertebral number unknown but in other

Psednos number of vertebrae usually is 6–8 more than the number of dorsal-fin rays; therefore, vertebral number probably is about 43.

Sensory System. Stein noted 2 nasal, 5 infraorbital, 6 preoperculo-mandibular pores ("Burke's pore formula 2–5–6–?") and a coronal pore. Some pores are clearly depicted (Fig. 14). Upper nasal pore above nostril and level with upper margin of eye. Four infraorbital pores in a line below eye [these seem to be io_{2-5}, the io_1 pore usually situated at beginning of suborbital bone projection is not shown on figure]. The io_6 pore behind posterodorsal margin of eye absent as in other *Psednos* with low vertebral counts and the coronal pore present. Two temporal pores are shown: t_1 pore above posterior edge of eye, another (suprabranchial) pore level with 1st but much higher and ahead from the upper end of gill slit. Last preoperculo-mandibular pore level with lower half of eye. Thus, there are 1 coronal, 2 nasal, 1+1 temporal, 5(5+0) infraorbital, and 6 preoperculo-mandibular pores.

Measurements and Counts. HL 24.5, bd 26.2 (107), preD 28.1, preA 43.6, snout to anus 23.4, UPL 13.6 (55.6), eye 6.8 (27.8% HL [but on picture about 20%]), snout 7.0 (28.9), maxillary 13.6 (55.6). V about 43, D 36, A 28, P 14(8+1+5), C 5 (?).

Color. "Skin tan or transparent. Body tan, inside of mouth, gill cavity, and peritoneum, dark brown. Stomach blackish." (Stein 1979: 7).

Distribution. Known only from the southwestern Indian Ocean, in the northern part of Crozet Basin near the Southwest Indian Ridge, midwater 0–350 m.

Etymology. Named after David L. Stein, American ichthyologist who originally described the specimen on which this species is based and who is well known for his research on liparid fishes.

Comparative Notes. Psednos steini belongs to a group of *Psednos* with low numbers of vertebrae (41–43, D 34–38), a coronal pore, 5(5+0) io pores, 1+1 temporal pores. Distinguished by a small, vertical gill slit (equal to eye) that is located high (dorsal end level with pupil), eye not less than 20% HL, pectoral fin with 14(8+1+5) rays and 1 notch ray; and a tan color. Most similar to *P. sargassicus* but differs in much larger eye (not less than 20% HL vs 15.4%), a gill slit equal to eye (vs 1.5 eye diameter), and a pale caudal part of body (vs tan). Stein (1979) described the holotype of *P. steini* using the name "*Paraliparis micrurus.*" He was the first to find specimens similar to *Psednos micrurus* since Barnard's 1927 description but a detailed comparison was difficult because the holotype was thought to be lost and only the poor original description was available (Barnard, 1927a,b). Stein thought that some differences between his specimens and *P. micrurus* were due to allometric growth, but now, the study of new comparative material shows that this is a distinct species.

SPECIES INCERTAE SEDIS

Psednos sp. 1

Psednos sp. 1 Andriashev, 1992: 15, figs. 3c, 8; 1993a: 12, fig. 2B. Based on BMNH 7709/76, 1 specimen 39 mm SL, south of Iceland, 55°59′N, 19°58′W, depth 1250–1500 m and BMNH 9801/60, 1 specimen SL 39 mm, off northern Spain, 41°57′N, 16°49′W, 985–1010 m.

Andriashev's *Psednos* sp. 1 was not described in detail because the specimens are in bad condition, but the diagnostic characters are clear, and it is included in the key. However, because these BMNH specimens were not seen during this study, and because no additional material was found, it is not being formally described here.

These specimens belong to a group of *Psednos* with few vertebrae (41–43) and no coronal pore. They differ from all other species of this group by the gill slit extending ventrally in front of 2–3 pectoral rays, and by a lower pectoral lobe that is longer than upper lobe. The other eastern North Atlantic congeners, *P. christinae* Andriashev and *P. andriashevi* sp. nov., belong to another group, with more verte-

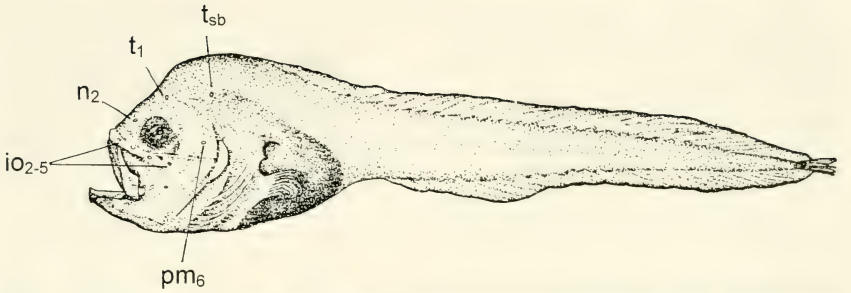

Figure 14. *Psednos steini* sp. nov. Male, 37 mm standard length. Holotype USNM 200488. Indian Ocean, Crozet Basin, 0–350 m (from Stein, 1979).

brae (47) and the coronal pore absent. Andriashev's species 1 has 43 vertebrae (9–10+33–34), D 38, A 31, P 14(9+5), C 6, lower pectoral lobe longer than upper lobe, and the coracoid has a strong handlelike projection.

DISCUSSION

The presence of 10 new species of *Psednos* in the Atlantic and Indian oceans and the expected existence of a few more undescribed species in other regions suggests that the genus *Psednos* is large and speciose, and has several species that are still undescribed. The species of *Psednos* are variable in meristic counts, in number and position of sensory pores, in the depth and width of head, in the extent of inclination of the mouth, in the size of eye, in the size and position of the gill slit, in the structure of pectoral fin and its girdle, and in pigmentation. Based on these characters, the known species of *Psednos* might be divided in two groups, as follows.

Group 1. Vertebrae 41–43, coronal pore present, infraorbital pores 5(5+0) (postorbital pore io_6 absent). Included are *P. micrurus, P. mirabilis, P. micruroides, P. microps, P. sagassicus, P. steini,* and *Psednos* sp. 1. However, the number of temporal pores varies in group 1; they are usually 1+1 (in *P. steini, P. mirabilis, P. sargassicus*), rarely 3–4 (in *P. micruroides*), or 0+1 (in *P. microps*). Species of this group occur in waters of South Africa (*P. micrurus*), the southwestern Indian Ocean (*P. steini, P. microps*), and also in the Atlantic: northern Sargasso Sea (*P. sargassicus*), off the slope of New England (*P. mirabilis*), waters southeast of Greenland (*P. micruroides*), and eastern North Atlantic (*Psednos* sp. 1). Undescribed *Psednos* sp. 2 (*sensu* Andriashev, 1992) from southern California and Baja California is also assigned to this group because it has a coronal pore.

Group 2. Vertebrae 47, coronal pore absent, infraorbital pores 6(5+1), temporal pores usually 1+1 (except *P. gelatinosus,* which has 1+2). Included in this group are *P. christinae, P. andriashevi, P. barnardi, P. groenlandicus, P. harteli,* and *P. gelatinosus.* The number of preoperculo-mandibular pores is variable in this group; the two known eastern North Atlantic species have 7 pores (*P. christinae* and *P. andriashevi*), whereas all western North Atlantic species have 6 pores (*P. barnardi, P. groenlandicus, P. gelatinosus, P. harteli*). All group 2 species occur in the North Atlantic.

The pectoral girdle has been studied only in *P. micrurus* (Andriashev, 1992, fig. 2), *P. andriashevi* (Andriashev, 1992, fig. 7), *Psednos* sp. 1 (Andriashev, 1992, fig. 8), and *P. christinae, P. groenlandicus, P. mirabilis,* and *P. sargassicus* in the present study. In all species studied, the cartilagi-

nous basal lamina is without fenestrae and 3 rounded, equally spaced radials are present. Differences between species are in a shape of scapula: with a handlelike projection in *P. christinae, P. andriashevi,* and *Psednos* sp. 1, or without a projection (which is fused within its body) in *P. groenlandicus, P. mirabilis, P. sargassicus,* and, obviously, in *P. micrurus.* The shape of the coracoid also varies: *Psednos* sp. 1 has a long handlelike projection, in *P. micrurus* it is short and wide, and the coracoid is half-moon shape and lacks a projection (which is fused with its body—see *P. sargassicus*) in *P. christinae, P. andriashevi, P. groenlandicus, P. mirabilis,* and *P. sargassicus.* The lower lobe of pectoral fin is usually shorter than the upper lobe but in *Psednos* sp. 1 and *P. andriashevi* the lower lobe is longer than the upper lobe. In addition, the pectoral notch usually has 1 or 2 rays, but they are lacking in *P. mirabilis.*

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